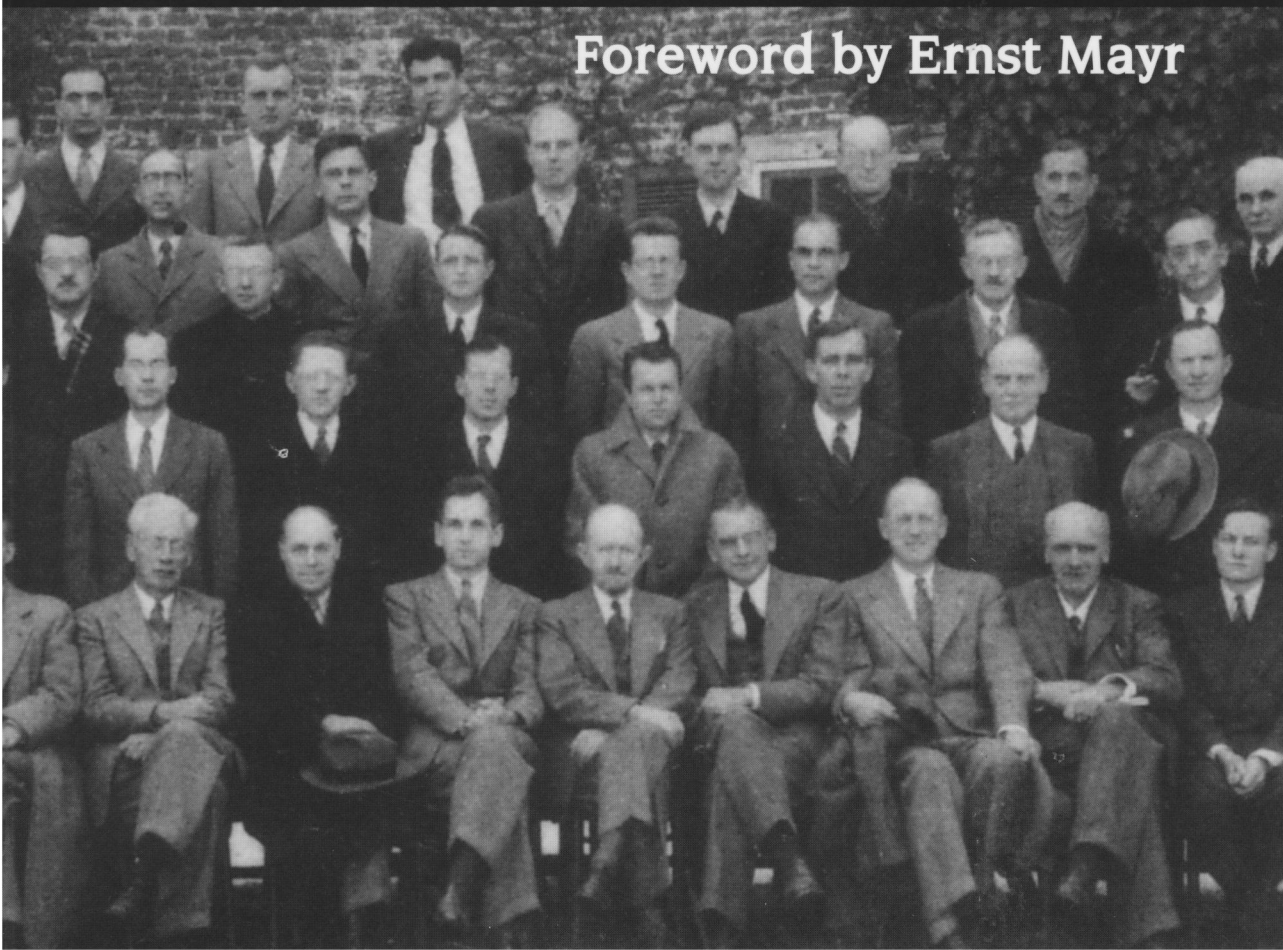


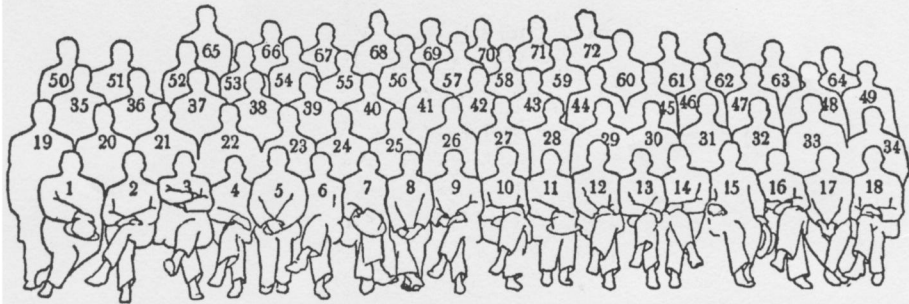
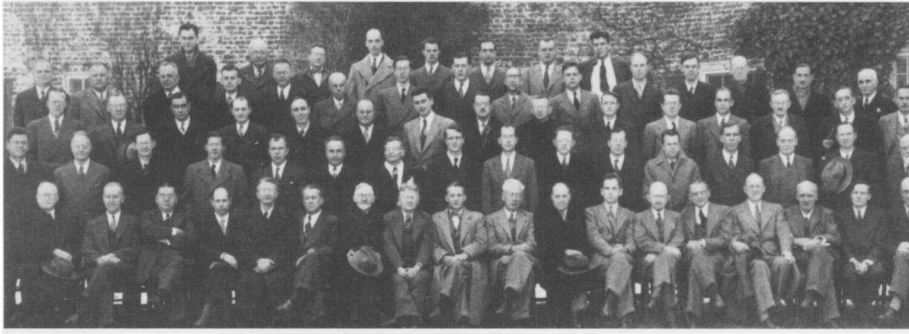
Exploring the Borderlands

Documents of the
Committee on Common Problems of
Genetics, Paleontology, and Systematics
1943-1944

Joe Cain

Foreword by Ernst Mayr





Group photograph from 1947 Princeton conference on "Genetics, Paleontology, and Evolution." The culmination of the National Research Council's Committee on Common Problems of Genetics, Paleontology, and Systematics, this conference also served to inaugurate the Society for the Study of Evolution. (Reproduced from Glenn Jepsen, "Genetics, Paleontology, and Evolution," Princeton University Bicentennial Conference, 1948, ser. 2, conf. 3, pp. 36–37.) Participants included:

- (1) Walter Hermann Bucher (2) Carl Owen Dunbar (3) Karl Patterson Schmidt (4) Curt Stern (5) Horace Elmer Wood, II (6) Charles Lewis Camp (7) Lee Raymond Dice (8) Sewall Wright (9) Glenn Lowell Jepsen (10) Alfred Henry Sturtevant (11) Hermann Joseph Muller (12) Ernst Mayr (13) George Gaylord Simpson (14) Alfred Sherwood Romer (15) Ralph Works Chaney. (16) John Burdon Sanderson (J. B. S.) Haldane (17) George Ledyard Stebbins, Jr. (18) Edmund Briscoe Ford (19) Carl Leavitt Hubbs (20) Carl Clawson Epling (21) Hiram Bentley Glass (22) William Hovanitz (23) Francis Joseph Ryan (24) Herbert Louis Mason (25) Maxim Konradovich Elias (26) Colin S. Pittendrigh (27) John Alexander Moore (28) Bobb Schaeffer (29) Joseph Tracy Gregory (30) Henry Nathaniel Andrews, Jr. (31) Erling Dorf (32) James Brookes Knight (33) Norman Dennis Newell (34) George Harrison Shull (35) Paul Orman McGrew (36) Arthur Bevan (37) Gustav Arthur Cooper (38) Arthur K. Miller (39) Edwin Harris Colbert (40) Ruben Arthur Stirton (41) John E. Pfeiffer (42) Delbert Dwight Davis (43) Theodor Karl Just (44) Francis Marion Ownbey (45) Charles Edward Wilde, Jr. (46) Patrick Mason Hurley (47) Arthur Francis Buddington (48) Lewis John Stadler (49) Emmett Reid Dunn (50) Millislav Demerec (51) Edgar Anderson (52) Theodosius Dobzhansky (53) Harrison Dailey Stalker (54) Warren Poppino Spencer (55) David Meredith Seares Watson (56) Charles Duncan Michener (57) Klaus Mampell (58) Tracey Morton Sonneborn (59) Gustav Heinrich Ralph von Koenigswald (60) David Lambert Lack (61) T. Stanley Westoll (62) Bryan Patterson (63) Harold Francis Blum (64) Otto Maria Heinrich Haas (65) Charles Mitchell Bogert (66) Benjamin Franklin Howell (67) Franklyn Bosworth Van Houten (68) F. L. Ferris, Jr. (69) Edward Novitski (70) Salvador Edward Luria (71) Steven K. Fox (72) Kenneth Willard Cooper

Attended but missing from photograph: George Wells Beadle Myron Gordon Adolph Knopf	Expected at conference but did not attend: Ernest Brown Babcock Donald Randolph Charles Nikolai Petrovich Dubinin Fred B. Phleger R. A. Silow
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EXPLORING THE BORDERLANDS

TRANSACTIONS
of the
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EXPLORING THE BORDERLANDS

DOCUMENTS OF THE
COMMITTEE ON COMMON PROBLEMS
OF GENETICS, PALEONTOLOGY,
AND SYSTEMATICS

Joe Cain
Editor

AMERICAN PHILOSOPHICAL SOCIETY
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2004

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CONTENTS

List of Tables	vii
Preface	ix
Foreword <i>Ernst Mayr</i>	xi
Historical Introduction <i>Joe Cain</i>	xiii
Editorial Notes <i>Joe Cain</i>	xxxix
Calendar of Correspondence	xli
Documents of the Committee on Common Problems	
Report of Meetings, October 1943	1
<i>Bulletin</i> 1: May 15, 1944	19
<i>Bulletin</i> 2: June 26, 1944	41
<i>Bulletin</i> 3: September 25, 1944	67
<i>Bulletin</i> 4: November 13, 1944	87
<i>Bulletin</i> 5: February 5, 1946	109
<i>Bulletin</i> 6: May 6, 1946	115
Appendices	
Appendix 1: Recruiting Letter for Committee	119
Appendix 2: Committee Mailing List	125
Appendix 3: "Reading List in Genetics"	127
Appendix 4: "Reading List in Paleontology"	129
Appendix 5: "Reading List in Systematics"	131
Appendix 6: Questionnaire	133
Appendix 7: "Reading List on Paleobotany"	135
Appendix 8: Abbreviations for Archive Materials	137
Bibliography	139
Name Index	149
Species Index	153
Subject Index	155

LIST OF TABLES

TABLE 1	Committee on Common Problems in Genetics and Paleontology, 2 October 1943	xxxvi
TABLE 2	Publications of the Committee on Common Problems in Genetics and Paleontology, 1943–1949	xxxvii
TABLE 3	Subject Threads in <i>Bulletins</i> 1–4	xxxviii
TABLE A1.1	“Tentative List” of Committee Members	122
TABLE A1.2	List of Possible Topics for Committee Attention	123

PREFACE

This volume reproduces one *Report of Meetings* and six *Bulletins* from the Committee on Common Problems of Genetics, Paleontology, and Systematics. This Committee operated as an administrative unit of the National Research Council (NRC), part of the US National Academy of Science. It was launched in 1943, blossomed for two years, then served as a cornerstone for other cooperative projects. These later projects included the journal *Evolution*, the Society for the Study of Evolution, and the 1947 Princeton conference on “genetics, paleontology, and evolution.” When discharging this Committee in 1949, NRC officials judged it an unqualified success.

Membership of the Committee on Common Problems included key contributors to reform of American evolutionary studies during the famous “synthesis” period, spanning the second quarter of the twentieth century. These reformers profoundly influenced later generations of evolutionary studies. Considerable debate surrounds historical questions concerning this group’s accomplishments: precisely what did they achieve, and how were these accomplishments secured? No matter how historians approach such questions, they always return to the Committee on Common Problems.

The documents reproduced in this volume have remained out of circulation since their original distribution in the 1940s. Bringing them out of storage offers an chance to examine firsthand the Committee’s activities. It also provides an opportunity to reconsider questions of motivation, interaction, and influence.

For permission to republish these documents, I thank the Archives of the US National Academy of Science (Washington, DC) and the American Philosophical Society (APS) Library (Philadelphia). A complete set of bulletins is located both in the Committee’s files at the Archives of the NAS and in the Simpson Papers at the APS Library. For his generous foreword and his long-time support, I thank Ernst Mayr. I’d also like to thank Martin Levitt, Roy Goodman, Rob Cox, Valerie-Anne Lutz, and Janice Goldblum. Especially valuable has been support from Rita Dockery and Jarvis Cain. This editorial project was completed while I held the Frederick H. Burkhardt Resident Fellowship in Evolutionary Biology at the American Philosophical Society Library. I heartily thank the Barra Foundation for its generosity in providing that fellowship. Some travel to archives was funded by a grant from the Royal Society.

This project is dedicated to the late Dr. Edward Carter II, Librarian of the American Philosophical Society. His fellowship and enthusiasm are sorely missed.

Joe Cain
May 2004

FOREWORD

Ernst Mayr

In the 1920s evolutionary biology seemed to be hopelessly split, and yet by the Princeton conference in 1947 a synthesis of the seemingly so divergent views had been achieved. Historians are vitally interested in how this could have been accomplished in such a short time. There were a number of mavericks, like Richard Goldschmidt, who had their own special theory of evolution. Overall, evolutionists were split into three camps: the (mathematical) population geneticists, the species-level taxonomists (“naturalists”), and the paleontologists. Each camp had its own history and subscribed to a special set of evolutionary theories.

The population geneticists originated with the T. H. Morgan research school at Columbia University. They stressed gradual evolution due to small mutations and they accepted natural selection. They opposed the early Mendelians (Bateson, De Vries, Johannson) who defended saltational evolution through large mutations and did not accept natural selection. Their views were unified in the 1930–1932 publications of R. A. Fisher, J. B. S. Haldane, and Sewall Wright. Their work unified the camp of the geneticists and could be called the Fisherian synthesis, after its prominent leader. This group dealt exclusively with genetic variation in a population. They completely neglected all problems of diversity, including macroevolution. It was up to the taxonomists to fill this gap. A first endeavor, the Society for the Study of Speciation, never developed owing to the war and the inactivity of its leader, Alfred Emerson. The efforts of other taxonomists were more successful, leading in 1946 to the founding of the Society for the Study of Evolution and the creation of the journal *Evolution* in 1947. This has been described in detail by Cain (2000).

This left out a third group of evolutionists, the paleontologists. They dealt with macroevolution, with fossil histories, and the causes of evolutionary changes. No other group of evolutionists was as divided as the paleontologists. Almost unanimously they rejected natural selection, and as a group, they were regrettably unaware of the advances that had been made by geneticists. Curiously it was a classical geologist, Walter Bucher at Columbia University, who decided something should be done about the backwardness of the paleontologists and who found a powerful ally in George Gaylord Simpson.

Joe Cain has given us an admirable account of the highly diverse activities that led first to the establishment of the Committee on Common Problems and its activities. Unfortunately, the war then broke out and necessitated a curtailment of all traveling and most other activities. The founding of a scientific newsletter, the Committee's *Bulletin*, succeeded in maintaining some continuity during this difficult period, until Simpson returned from military service. Perhaps his absence was serendipitous because Dobzhansky (genetics) and Mayr (systematics) had considerably widened the sphere of interest of the Committee beyond paleontology. This established the basis for the founding of the Society for the Study of Evolution. By the time of the wind-up of the Committee through the Princeton conference, a unified science of evolutionary biology had come into being. For the historian there is no question the Committee's establishment and activity were crucial in the creation of the field of evolutionary biology and that this was one of the key events in the history of modern biology.

We are grateful to Joe Cain for bringing this important material to light and particularly for making the four issues of the Bulletins available in print. They played a crucial role in the founding of the journal *Evolution* and the Society for the Study of Evolution. These in turn were the decisive event in the establishment of evolutionary biology as part of modern biology.

Ernst Mayr
May 2004

HISTORICAL INTRODUCTION

Joe Cain

The Committee on Common Problems in Genetics, Paleontology and Systematics (CCP) operated between 1943 and 1949. These previously unpublished documents circulated in the 1940s as records of the Committee's intellectual activity. Four reasons justify reproducing them.

First, the CCP offers a benchmark during an important transition in American evolutionary studies. Cooperative groups certainly existed in evolutionary studies before this Committee formed.¹ However, the CCP was the first organized assertion of common interest by the self-described “architects” of the American synthesis period, including Theodosius Dobzhansky, George Gaylord Simpson, and Ernst Mayr. These researchers hoped the CCP would support their particular designs for interdisciplinary exchanges of knowledge, practice, and perspective. The CCP also was unusual among cooperative groups in this period because it sought both a national scale for their network and an exchange of information well beyond the social circles of its organizers.²

As a benchmark, the CCP also illustrates important tensions within the American community of evolutionary studies during the synthesis period. By and large these tensions have gone unnoticed among historians. Though agreed on their strategic goals, Committee members differed when translating these goals into practice and when making choices as to which problems deserved a place at the Committee's intellectual heart. These different priorities operated within a broad agreement that the Committee mechanism served useful purposes. Not surprisingly, as the Committee leadership changed hands, priorities and implementation changed too. A close study of the CCP's work reminds us that interdisciplinary projects normally involve multiple perspectives and polyvalence. In this way, the CCP's synthesis represented more a coalition than merger (Cain 2003).

A second reason for reproducing core CCP documents is to simplify access to important resources from the synthesis period. In the past, historians of this period in evolutionary studies have tied

1. A good example is the biosystematics group in the San Francisco bay area, see recollections by Lidicker (2000) and historical studies by Smocovitis (1988) and Hagen (1981).

2. National organization also was a goal for some backers of the Society for the Study of Speciation, launched in 1939 but sputtering through 1940 and quiescent from 1941, *see* Cain (2000b).

themselves too closely to a small number of published texts, especially the evolution texts of the Columbia Biological Series (Dobzhansky 1937; Mayr 1942; Simpson 1944; Stebbins 1950; on this series, see Cain 2001). For many years the only published material of substance about the CCP was Jepsen (1949), the foreword to *Genetics, Paleontology, and Evolution* (Jepsen, Mayr and Simpson 1949). This self-congratulatory retrospective provides little more than highlights of Committee successes. For the historian it obscures more than it enlightens. Resurrecting source documents from the CCP supports the long-term goal of increasing the breadth of primary sources used in studies of the synthesis period. These documents never circulated widely, and only a few copies remain in archival collections. They are too important to lose.

Third, while I've written a good deal on how the New York circle organized the CCP and planned related activities, I've provided no substantial account of the intellectual and empirical substance that eventually flowed through these mechanisms (Cain 2002). This creates a rather one-sided image of the Committee's value. The CCP was more than a shrewd political mechanism for promoting certain types of exchange or for defining problems in self-serving ways. Ideas, practice, and evidence flowed through the CCP. As a result, arguments were fostered, hypothesis testing took place, and research projects moved forward.

Texts do not speak for themselves. Still, these documents capture moments of collegial exchange, question setting, exploration, and pontification at a time when experts were re-negotiating the boundaries of evolutionary studies and making decisions about the robustness of its many research programs. No exegesis can capture the multiple layers of communication at work in these original exchanges. The wisest course of action for me as a scholar is to move these documents to the foreground and encourage others to examine them firsthand.

Finally, these documents provide additional primary materials for specialized historical projects—regardless of the analytical perspective a historian might use to digest them. Importantly, some writing appears nowhere other than in these documents. Moreover, following the *Bulletins* permits the monitoring of participation by various subsets within the collective enterprise. Though it is a distant goal, I hope evolutionary biologists can find in this project sparks to ignite a fresh perspective in their own research.

The CCP's life history can be divided into three phases:

1. organization and first meetings (1941–end of 1943): culminating in the *Report of Meetings*
2. interaction through correspondence (1944): producing *Bulletins* 1–4
3. platform for other projects: producing *Bulletins* 5–6 and involvement with the Princeton conference, the Society for the Study of Evolution, and the journal, *Evolution*.

Cain (1993; 2002) describes the CCP's launch and operation in detail. The sections that follow briefly describe the Committee's institutional context, then survey each of the above phases.

■ 1. *Institutional context*

The CCP operated under the administrative auspices of the National Research Council (NRC). It was a cooperative venture between the NRC Division of Biology and Agriculture and the NRC Division of Geology and Geography, with the latter assuming managerial oversight. When formally authorized in February 1943, the original Committee carried the title, "Committee on Common Problems in Genetics and Paleontology." It was one of more than thirty committees in the Division of Geology and Geography during the early and mid-1940s.

Division chairman Walter Bucher described the CCP's purpose in straightforward terms: "to further the cooperation of the students of the two fields and to acquaint the workers in either field with the methods and resources in the other field. Many phases of the study of evolution concern geneticists and paleontologists equally, and the need for a closer cooperation has become increasingly apparent in recent years."³ In his annual report for 1943, Bucher added vision:

The nature of short-range changes has been shown in startling new light by the discoveries of genetics, while paleontology has produced a wealth of new material, capable of quantitative analysis, which is beginning to shed light on the long-range changes. The two fields are clearly complementary. But each science has developed a nomenclature and a technique of such intricacy that many workers in the two fields have lost contact with each other.⁴

By design, CCP members were assigned two labels (Table 1). One label was geographical. The Committee operated in two functionally distinct geographical groups: Eastern (based in New York, focusing on zoological issues) and Western (based in Berkeley, focusing on botanical issues, and little more than a re-labeling of the biosystematics group). The other label was disciplinary: geneticists and paleontologists. Each regional group had representatives from both disciplines. Disciplinary distinctions were construed in the broadest

3. Notice in "Report of the Committee on Common Problems of Genetics and Paleontology," in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1," 1 June 1943. This was a revision to the annual report (Appendix N) given to the division director, in NRC Archives, folder "Geology and Geography. 1943. Committee on Common Problems in Genetics and Paleontology." The request for appointment and funding is Bucher to Harrison or Kenerson, "Bimonthly Report of the Chairman, Division of Geology and Geography for December [1942]—January [1943]," 17 February 1943 in NAS Archives, folder "Geology and Geography. 1943. Reports of Administrative Committee."

4. Walter Bucher's "Report of the Chairman of the Division of Geology and Geography for the Year 1942–1943," on p. 10 in NAS Archives, folder "Geology and Geography. Annual Report. 1943."

terms. They rarely affected Committee work; by mid 1944, they were irrelevant.

The Committee's name changed in April 1944 following a request by Ernst Mayr. As he rose to prominence in the Committee's operations, Mayr complained that the CCP's original name failed to capture the emerging cooperative work of geneticists and paleontologists, together with systematists and ecologists. It also ignored, he said, the crucial role played by members of his own professional community in linking these two groups together. He asked the NRC to recognize "systematics" as a partner—the "vital link"—in the Committee's work.⁵

During recent discussions [among CCP leaders], the fact was recognized that the field of systematics is actually an integral part of the scope of our Committee. The geneticists, for example, who are on the Committee are not, so to speak, a random sample of all geneticists but are those who are working in the border zone between genetics and systematics. In fact, some of the members [...] are systematists rather than geneticists. All paleontologists are, of course, also systematists. It is for these reasons that the Committee plans to ask the [NRC] to change our name to that of "Committee on Common Problems of Genetics, Paleontology, and Systematics."⁶

NRC officials accepted this argument and changed the CCP's name at the next opportunity.

2. *Origins of the CCP and its first meetings*

The CCP was initiated by paleontologists seeking interaction with geneticists. This first involved a trio of friends: George Gaylord Simpson, Glenn Lowell Jepsen, and Horace Elmer Wood, 2nd. They sought interaction with geneticists for several reasons.

First, this trio placed themselves among a group of modernizers within paleontology.⁷ They represented their field as a biologist's program. They wanted interest shifted towards biological processes and

5. The "vital link" quote is located in Appendix H, [CCP] Annual Report, 29 April 1944, on p. 2 in NAS Archives, folder "Geology and Geography. 1944. Committee on Common Problems of Genetics, Paleontology and Systematics."

6. Babcock, Bucher, Chaney, Dobzhansky, Jepsen, Mayr to Simpson 21 January 1944 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1."

7. These "modern" paleontologists would contrast themselves with some in the previous generation, such as H.F. Osborn or W.B. Scott, but would attach themselves to others, such as W.D. Matthew and W.K. Gregory. This transition in America has yet to be critically studied. Bowler (1996) discusses a similar distinction between generations in British paleontology. The effort to modernize paleontology also was behind Simpson's role in co-organizing the Society of Vertebrate Paleontology in 1940 and Jepsen's role as its president several years later (Cain 1990; Wilson 1990). Simpson made a strong leader in this confidence-building work (Cain 1992; Ruse 1996; Laporte 2000). His Fort Union work and statistical applications were examples of his deployment of methodological changes widely used by experimentalists (Simpson 1937a).

mechanisms in which the study of form and identification served as means to other ends.

To further this enterprise, *modern* paleontologists worked to interpret paleontological observations through the lens of up-to-date biological knowledge. They also sought to assess explanations of paleontological phenomena by the epistemic standards of their biologist colleagues. A committee mixing paleontologists and geneticists offered this trio a means for simplifying access to communities of modern biologists and modern biological practice. It served as a “transitional group” (*sensu* Bruffee 1993), and perhaps extend their modernization into new areas or to new colleagues.

Second, these paleontologists argued geneticists poorly understood modern paleontology, both in terms of its epistemic foundations and in terms of its value for understanding biological phenomena. As Bucher first described the Committee idea, “The prime purpose ... is mutual enlightenment concerning the factual basis of theoretical concepts and interpretations.” This trio hoped to increase the interaction between competent and receptive colleagues: a few reputable paleontologists—those “with a good biological background” who also took “an active interest in the specific aspects of evolution”—and a few geneticists “actively interested in a rapprochement of workers in genetics and in paleontology.” This exchange also offered opportunities for confidence building across the fence. At least some geneticists would meet paleontologists interested in contemporary biology and working to be taken seriously.⁸

Third, this paleontologist trio hoped to create a more symmetrical relationship between paleontologists and geneticists in the study of fundamental biological problems. By the time the Committee was charged, Simpson had completed his manuscript for *Tempo and Mode in Evolution*, (Simpson 1944) and his essay on systematics (Simpson 1945b). He had gone so far as to identify point mutations in a fossil series (Simpson 1944: 43) and resolve speciation events in paleontological horizons (Simpson 1937). Simpson also placed paleontologists in an assessment role for explanations in genetics and population genetics.

...only the paleontologist can hope to learn whether the principles determined in the laboratory are indeed valid in the larger field, whether additional principles must be invoked and if so, what they are. (Simpson 1944: xvii)

Jepsen (1944; 1946) celebrated this work and repeated calls to extend collaborations. This trio hoped to press beyond the biologist’s emphasis on speciation and infra-specific phenomena and toward evolutionary questions where paleontologists could best contribute.

8. Bucher to Executive Committee, Division of Geology and Geography 22 December 1942 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #1.”

Examples included evolutionary rates and the origins of higher taxonomic categories.⁹

No evidence suggests this trio seriously discussed forming an interdisciplinary group before their first serious invitation came in December 1941. That month, at a meeting of the Geological Society of America, these three paleontologists heard Walter Bucher's keynote address in which he promoted the virtues of interdisciplinary collaborations and "borderland" research (Bucher 1942). Bucher offered NRC support—funds and logistical aid—for nearly any type of interdisciplinary research relevant to his division.¹⁰ Among a long list of examples, he specifically mentioned Simpson and his interdisciplinary exchanges on the subject of speciation. He called on paleontologists to extend Simpson's example and offered NRC support to anyone willing to step forward. The prospect of specific patronage inspired these paleontologists to act.

Bucher's suggestion of an interdisciplinary committee was not out of the ordinary for a chair of NRC divisions.¹¹ The NRC made frequent use of interdisciplinary committees of the kind Bucher proposed. For instance, the CCP followed closely behind efforts within the Division of Geology and Geography to encourage collaborative projects in paleoecology via the "Committee on Marine Ecology as Related to Paleontology." As its chair, Harry S. Ladd, explained, "The purpose of this Committee is to make available to paleontologists information concerning new developments in modern ecology and to stimulate cooperation between ecologists and paleontologists in the study of paleoecological problems."¹²

Simpson's original plan for studying common problems within a committee framework identified pairs of collaborators across the US: one geneticist and one paleontologist. Proximity was the key, and he preferred pairs located in the same city: for example, Sewall Wright and

9. Not surprisingly, these were central topics in Simpson (1944) and his other work (e.g., Simpson 1937a; 1937b; 1937c; 1943).

10. Bucher's (1942) offer was made to all scientists present at the conference he was attending—the Geological Society of America—and came immediately after America's formal declaration of war in 1941. The call for cooperation and facilitation was directed at more than these three paleontologists. Bugos (1989) argued the NRC positioned itself as an agent of interdisciplinary collaboration as a deliberate corporate strategy, creating a virtue in one of the services it was best placed to provide.

11. The prospect for an interdisciplinary committee between paleontologists and geneticists also was received sympathetically by Robert Griggs, Chairman for the NRC's Division of Biology and Agriculture. Griggs (1939) publicly lamented the presence of "hostile camps" within evolutionary studies and sought ways to reconcile paleontologists and geneticists in their views.

12. The paleoecology project is presented in Walter Bucher, "Report of the Chairman of the Division of Geology and Geography for the Year 1942–1943" in NAS Archives, folder "Geology and Geography, Annual Report 1943." Quote on p. 8. This project took its inspiration from an earlier NRC committee on paleoecology, chaired by William Henry Twenhofel between 1934–1937, and a program described by Vaughan (1940) as retiring president of the Geological Society of America. The resulting subcommittee on the ecology of marine organisms (later renamed at the committee level), chaired by Harry S. Ladd, 1940–1957, produced two influential documents: Hedgpeth (1957) and Ladd (1957). Regular reports of the group's work are in NAS Archives.

Bryan Patterson in Chicago. Simpson wanted individuals who could consult each other with ease.¹³ One-to-one contact structured professional exchange in a way Simpson, himself, found most comfortable. He detested large conferences and thought the presentation of formal papers rarely led to meaningful exchange.

During 1942, Simpson developed this scheme of collaborative pairs in consultation with three sets of colleagues: (1) Jepsen and Wood, (2) Bucher, and (3) Dobzhansky. He also brought others into the planning as needed. In October 1942 this group co-opted the fiftieth anniversary of the Columbia University's Department of Zoology for a roundtable discussion of this idea. (Many at this roundtable later were invited to join the Committee.) No minutes of the discussion were kept, but this sounding of opinion suggested enthusiastic support for the committee idea. The next step was a formal proposal to the NRC.

In the midst of drafting a formal proposal, Simpson entered military service, leaving New York in December 1942.¹⁴ In his absence, Simpson appointed Jepsen as his proxy: to complete the organization and put their plan into effect. Jepsen's own interests subverted Simpson's original plans. One-to-one collaborations would not have served Jepsen well. He sought a break from relative isolation in Princeton and wanted to interact with distinguished colleagues on a national scale. Together, Jepsen, Dobzhansky, and Bucher agreed to abandon Simpson's one-to-one plan in favor of a collective, committee-type structure. They proposed this plan to the NRC, which accepted it and allocated a small fund for travel and administrative expenses.¹⁵

Once they received formal approval, Committee organizers posted a recruiting letter (Appendix 1) to build their Committee's membership. In this letter, they stressed the need for paleontologists to become "better acquainted with the methods of working and especially the essential results of geneticists...." Conversely, they stressed the need for geneticists to better appreciate "the degree of reliability obtained by stratigraphic and paleontologic methods and the validity of generalizations secured by paleontologists." Thus, the Committee was to enable a "meeting of minds working along the boundary of these two fields."¹⁶

13. The selection of these pairs is discussed in Cain (1993).

14. Simpson entered military service in early December 1942 after volunteering. He served in the North African, Sicilian, and Italian campaigns (Simpson 1978; Roe 1986; Laporte 1987). There is no evidence he contributed to Committee business during his absence, though he corresponded irregularly with colleagues at the American Museum. Simpson returned to Committee work in September or October 1944 and attended a meeting of the Steering Committee in October (Mayr to Stebbins 1 November 1944 in Mayr Papers, folder 105). See also Simpson's introductory remarks in *Bulletin* 4, dated 13 November 1944. Some of Simpson's activities in military service were reported in the *Society of Vertebrate Paleontology News Bulletin* 9: 7–8; 10: 5; 11: 5.

15. Bucher to Executive Committee, Division of Geology and Geography 22 December 1942 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1."

16. Dobzhansky, Jepsen, and Bucher to "Colleague" 26 February 1943 in NAS Archives, folder "Geology and Geography. 1943. Committee on Common Problems of Genetics and Paleontology."

Dobzhansky left the Committee's leadership shortly after its formal organization when an opportunity arose for him to undertake *Drosophila* fieldwork in Brasil and promote population genetics in São Paulo.¹⁷ Dobzhansky appointed Ernst Mayr as his proxy on the CCP. As with Jepsen, Mayr preferred a committee structure based on group work. More important, he asserted himself within the Committee in ways Dobzhansky never would.

■ 3. *Producing Publications: The Report of Meetings and Bulletins*

When the NRC created the CCP in February 1943 several basic points were agreed. First, the organization was structured in a more-or-less standard committee format (Table 1). Second, they agreed to organize a series of conferences in which the whole CCP would interact. Third, the Committee would work its way organically through the borderland between genetics and paleontology, slowly developing topics for analysis and mutual assistance. Fourth, after a period of exploration, the Committee would hold a final conference and produce some kind of consensus statement. Much of this ran against Simpson's original preference for one-to-one collaborations. Because he was away from the process, however, these alternative schemes rose to the front. Indeed, though Simpson was the creative force behind the Committee's initial concept, others deserve credit for implementing the CCP and driving it towards significant results. This is especially true for the meetings held in 1943 and the first four *Bulletins*. (A list of products is provided in Table 2.)

National travel restrictions frustrated intentions to organize full CCP meetings during the war. Rather than simply suspend the Committee indefinitely, its leaders instead chose to organize regional meetings during the summer of 1943.¹⁸ These were planned by Babcock and Stebbins on the West Coast, and by Jepsen and Mayr on the East Coast. Such meetings involved long-distance travel only for a few Committee members.

These meetings started the Committee's collective work and made some progress towards project definition. What, after all, were their common problems and principal needs for exchange?

The Report of Meetings, 1943

The *Report* describes activities at the CCP's regional meetings held in June and July 1943. It was compiled several months afterwards and

17. Dobzhansky spent four months in São Paulo and two months collecting in the field under the auspices of a "good neighbors" program for the Committee on Inter-American Artistic and Intellectual Relations, a division within the Office of the Coordinator of Inter-American Affairs of the U.S. government. See Dobzhansky to Wright 26 January 1943 in Wright Papers, folder "Dobzhansky, Theodosius, 1943-1944."

18. The split meetings were planned as early as Bucher to Executive Committee, Division of Geology and Geography 22 December 1942 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1."

was not anticipated at the time of the meetings.¹⁹ Only one *Report* was produced over the Committee's lifespan because only one set of formal regional meetings was held before the Committee dissolved.

Circulated in October 1943, the *Report* is structured in halves. One half provides a synopsis of the Western group's meeting: four sessions, each built around a principal speaker and discussion. Brief mention is given to minor points of CCP business. The second half of the *Report* describes the Eastern group's meeting: a program of formal presentations, abstracts of those presentations, and the report of a substantial business meeting in which Committee-wide projects were discussed.

Several features of the *Report* are noteworthy. First, the work described for the Western and Eastern groups is strikingly different. This suggests relative independence when undertaking the Committee's task. Second, the report from the Western group shows a high degree of informality and integration. Participants in the Western group seemed more familiar with each other before the Committee; the boundaries between paleontology and genetics seemed far less distinct. Indeed, some in the Western group already participated in the kinds of collaboration sought in the CCP's charge.

In contrast, the Eastern group seemed poorly integrated. Group members were less familiar personally with each other. The presentations show a formality suggesting multiple monologues rather than exchange. The Eastern group also reported much more Committee-level business. This likely was due to the fact that CCP's organizers were based in New York. They used the Eastern meeting to consider the Committee's broader aim and purpose, as well as ancillary projects. Overall, it's hard to avoid the impression that the leaders of the Eastern group considered this Committee largely their own project. They asserted helmsmanship. Likewise, it's hard to understand what extra value CCP activity brought to the Western group aside from the opportunity to defray travel costs for visits from a few familiar colleagues.

No evidence speaks to the question of who decided to create the *Report of Meetings*. At least two motivations, no doubt, were involved. One was bureaucratic. The CCP operated within NRC administration. NRC administrators required regular progress reports and evidence of activity. For another reason, the two groups needed some way to communicate. An inexpensive circular probably seemed an easy solution.

19. Anticipation of a *Report* is not mentioned in the annual report for the NRC produced in the 1 June 1943 Report of the Committee on Common Problems of Genetics and Paleontology in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1." The CCP was not the only committee in the Division of Geology and Geography circulating mimeographed reports in lieu of meetings, see 2 December 1944 "Interim Report of [the Division] for period October–November," in NAS Archives, folder "Geology and Geography. General: 1944" in which the Committee on Marine Ecology as Related to Paleontology is reported using this technique.

Though Mayr claimed to be merely “an administrator” in Dobzhansky’s absence, he took active charge of the Eastern group of geneticists while organizing the summer meeting. Afterwards, he attempted to lead them forward. The *Report* shows lingering influences of Simpson’s original plan for CCP activity, but Mayr’s priorities were in the forefront by the appearance of the Committee’s first *Bulletin*. His intellectual goals for the CCP emphasized inter-disciplinary studies of speciation processes, especially in zoology (e.g., Mayr 1940; 1941; 1942). Equally important, he had long sought mechanisms for exchange and interaction with colleagues across the spectrum of biological specialties. The multi-disciplinary nature of the CCP offered precisely this setting for him.²⁰

Of the proxies who stepped in to lead the CCP Mayr had the largest impact on its subsequent activity. Bucher served only as a placeholder for Simpson. Jepsen took a defensive stand and pressed principally for a recognition by geneticists of paleontology’s legitimacy as a biological discipline (Jepsen 1944; 1946).

Mayr was never one merely to hold a place for Dobzhansky’s return. He took the initiative. After the summer meetings in 1943, for instance, he pressed others in the genetics section to produce materials for exchange. Writing to Curt Stern a month after the Eastern group’s meeting, Mayr described the potential he saw in creating a permanent mechanism for exchange:

Everybody seems to feel that something worthwhile was accomplished and that it is necessary to follow the conference up by other efforts to further the mutual understanding of geneticists and paleontologists. The wish has been expressed by several of the paleontologists to be able to read leisurely the contributions of the geneticists and I have been thinking of preparing a circulating letter to be sent to all the paleontologists. This letter would consist of all the manuscripts of the geneticists that we can get hold of. Each paleontologist would then be asked to make his comments and in particular to state which of the information is of particular use to him and where he thinks a conflict exists between the information of the two fields. Such statements would be very valuable for the preparation of future meetings

20. From the start, Mayr actively engaged in Committee work: compare his and Jepsen’s reports in 1 June 1943 Report of the Committee on Common Problems of Genetics and Paleontology in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #1.” Mayr had wanted to promote this kind of activity through the Society for the Study of Speciation when it formed in 1939. When that group went silent after a first set of publications Mayr tried to organize a change in leadership but was stopped by Dobzhansky, who worried about keeping the speciation group on friendly terms (Cain 2000b). Since these events, Mayr had been waiting for an opportunity. Cain (2002: 293–297) argues speciation studies were but the most recent domain in which Mayr tried such organizing.

or possibly even of a public symposium. I realize that the manuscripts of the participating geneticists were not prepared in such a way as to be available for publication, or maybe even circulation, but I believe that even a handwritten copy would be of value in this connection. Any kind of a manuscript or collection of notes that you may have available would be useful for this purpose.²¹

Hoping to lead by example, Mayr circulated his own presentation on “discontinuity.” However, this produced nothing similar from other members of the section.²² The exchanges he so eagerly anticipated had collapsed.

Creating the Bulletins

After his suggestion for circulating manuscripts from the regional meeting failed, Mayr proposed a slightly more elaborate scheme for communication.

Questions are to be formulated by each member covering fundamental problems needing discussion and elucidation. These are to be distributed to all members with an invitation to those competent to deal with any one of the questions to reply in writing to the original author devoting not more than ten typewritten pages to one item. Copies of the letters and replies are to be distributed to all members at suitable intervals in the form of mimeographed bulletins.²³

This plan developed in December 1943. Mayr created his list of questions, but it’s not clear if anyone followed his second attempt to lead. By the end of January 1944, this second plan was streamlined into a project simply to encourage correspondence between CCP members and to reprint these exchanges, by means of a mimeographed circular, for distribution to the whole Committee.²⁴ Describing the idea to Stern, Mayr recommended, “... members of the Committee should correspond with each other concerning unsolved or otherwise obscure problems within the scope of the Committee.”²⁵ Dobzhansky was drafted into launching an inquisitive exchange with Chaney. This became the first subject for the circulars. Mayr volunteered as “central agency” for all exchanges. Promoting along the way, he had sufficient

21. Mayr to Stern 26 August 1943 in Stern Papers, folder “Mayr, Ernst #1.”

22. Mayr’s 14-page manuscript on discontinuity is preserved in folder “Mayr, Ernst #1” in Stern Papers. Muller produced a sketch, *see* Mayr Papers, folder 82.

23. Appendix H, [CCP] Annual Report, 29 April 1944, p. 2 in NAS Archives, folder “Geology and Geography. 1944. Committee on Common Problems of Genetics, Paleontology and Systematics.”

24. Babcock, Bucher, Chaney, Dobzhansky, Jepsen, Mayr to Simpson 21 January 1944 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #1.” Portions are reprinted as a preface to the Committee’s first *Bulletin*.

25. Mayr to Stern, 7 March 1944 in Stern Papers, folder “Mayr, Ernst #1.”

material to produce the first *Bulletin* of correspondence in May 1944.²⁶

Overall, Mayr created four *Bulletins* of correspondence over the middle six months of 1944. Material for a fifth was collected, but *Bulletin* 5 shifted into a different direction. (Table 3 lists the correspondence threads and a Calendar of Correspondence follows the Editorial Notes below.)

On their surface, the *Bulletins* maintained activity within the Committee: preserving momentum until such time as travel restrictions lifted and the CCP could meet as a whole. These letters also helped organizers build an agenda for the final CCP conference after the war.²⁷ In addition, Mayr used these *Bulletins* to demonstrate the idea that a community of discourse could be formed to discuss the interface between evolution and systematics. As Simpson, Jepsen, and Wood had with paleontology, Mayr had an agenda to modernize the connections between systematics and other biological specialties and to shift interest from zoological objects to biological processes (Mayr 1942; 1943; 1946; 1948). The CCP offered him a mechanism for promoting this agenda. The *Bulletins* provided a demonstration of its potential. Before long Mayr was sufficiently confident to scheme towards a “Journal of Animal Taxonomy.”²⁸ During six weeks at Cold Spring Harbor in the summer of 1944, he debated with Dobzhansky about taking over Emerson’s Society for the Study of Speciation (not functioning since 1941), or “founding a Society for the Study of Evolution which could be made the immediate successor to our Committee.”²⁹ Dobzhansky dissuaded him temporarily, citing politics within the profession. Mayr kept this option open, however, should an opportunity present itself in the future.

4. *Extensions and Capstone Projects*

After four *Bulletins*, the CCP’s activity abruptly changed. Simpson returned to the Committee’s chair in Autumn 1944 and reasserted control over its direction. First, he stopped the letter exchanges, arguing this informal approach “had been rather completely exploited.” Second, Simpson wanted to shift the CCP’s overall focus back to its paleontologist origins. In his hastily added “Preface” to Mayr’s fourth *Bulletin*, Simpson suggested this series “has accomplished a great deal

26. For an example of Mayr’s recruiting, see Mayr to Stern, 7 March 1944 in Stern Papers, folder “Mayr, Ernst #1.”

27. Simpson to Mayr 6 December 1944 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #1.” See also William Rubey (new chair of Division of Geology and Geography) to Harrison, 17 December 1943 in NAS Archives, folder “1943. Committee on Common Problems of Genetics and Paleontology.”

28. Mayr discussed his plan for a “Journal of Animal Taxonomy” with A. Glenn Richards in May 1944; see Mayr Papers, folder 104.

29. Mayr to Elias 14 August 1944 in Mayr Papers, folder 95.

more than the expression of a few facts and opinions, useful as these have also been.”

From the whole series of letters in the *Bulletin* there has emerged concrete evidence that a field common to the disciplines of genetics, paleontology, and systematics does really exist and this field is beginning to be clearly defined. Some, at least, of the more hopeful approaches to these common problems are indicated and exemplified. The existence of geneticists, paleontologists, and systematists interested in these problems and competent to attack them has been demonstrated. Their interest has been stimulated and made more concrete and their competence in the joint field has been increased by the exchange of views with students of other specialties. Thus great progress toward the goal of the Committee has been made.³⁰

By the end of 1944, the Committee's leadership had shifted their rhetoric. The *Bulletins* became evidence for the possibilities likely to come from the creation of more permanent facilities for exchange. Clearly, the perception of needs late in 1944 was different from early 1942. It had shifted from a desire to secure legitimacy and promote reform to a desire for pursuing the intellectual work of particular collaborations. Their rapprochement secure, Committee leaders suggested it was time for the CCP to “graduate.”³¹

Besides, Simpson was eager for closure by early 1946, when *Bulletin* 5 appeared. He wanted to end the administrative burdens of CCP work because other opportunities were making themselves available.³² It was time to move on. With slightly revised recollections Simpson explained the CCP was created only as an exploratory mechanism. Shortly after his leave from military service in Autumn 1944, Simpson asked the CCP's leadership to discuss “the future of the Committee.” Though his introductory remarks to *Bulletin* 4 encouraged continued correspondence, Simpson also wrote of the need to prepare “a more concrete statement of the final aim” for the Committee as a whole.

In 1945 the CCP stopped functioning as a collective project. Informal gatherings occasionally brought those in the regional sections together, but no formal meetings were organized. Collecting more correspondence for the *Bulletins* ceased, too. Activity shifted into other directions. Three projects later referred back to the CCP for legitimacy

30. Quote from Simpson's “Introductory Remarks” in *Bulletin* no. 4.

31. Mayr to Jepsen 6 February 1946 in Mayr Papers, folder 133. He also uses this phrase in Mayr to Griggs 28 December 1945 in NAS Archives, folder “Geology and Geography. 1946. Committee on Common Problems of Genetics, Paleontology and Systematics. It w/ Division of Biology and Agriculture.” The process of creating a new society is discussed in Cain (1994).

32. Simpson to Rubey 22 January 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3.”

but for all intents and purposes they were independent, stand-alone activities.

A New Society and Journal in Evolutionary Studies

From the CCP arose the confidence and opportunity to launch the journal, *Evolution*, and the supporting Society for the Study of Evolution (Cain 1994; 2000a; 2002). Mayr spearheaded these projects, coordinating with Dobzhansky and Simpson, as well as with many others. Mayr and Dobzhansky discussed the situation with Julian Huxley while he visited New York in December 1945.³³ They agreed the need for action in this dynamic moment in American science outweighed the politic risks of preempting Emerson should he ever decide to revive the speculation society.

The New York circle moved quickly. By the AAAS meeting in spring 1946 they had concrete proposals for a society and three options for a journal. NRC officials encouraged these developments and offered affiliation through the CCP. Funding to underwrite the journal proved difficult to arrange. After considerable maneuvering it arrived in November 1946. The first issue of *Evolution* appeared in mid-1947.

The Conference at Princeton University

The third activity connected with the Committee was the conference on “genetics, paleontology, and evolution” held in January 1947 at Princeton University as part of its bicentennial celebrations. Summaries of the conference proceedings circulated widely (Jepsen 1948). Contributed papers were published two years later (Jepsen, et al. 1949). No substantive historical study has been produced on the conference itself. The relation between the CCP and the Princeton conference is complicated. Indeed, a commitment to Princeton came late in the process of the CCP organizing its final meeting. This section reconstructs the basic chronology.

From the Committee’s start, CCP leaders expected to organize a conference and publish a summary statement of their collaborative work. Simpson would have held this after a long period of collaboration by his research pairs. The others expected each regional group to generate leads for meetings of the full Committee after war’s end. Such hopes were hampered by transportation difficulties, of course, and this led to the *Bulletins*. Hopes also were hampered by a genuine lack of clarity about conference topics once the Committee agreed on the success of their rapprochement.

In his April 1945 annual report to the NRC, Simpson was nonspecific about conference plans. He said the long-term goal of producing “a

33. Mayr and Huxley discussed the idea of a replacement society several times, such as Mayr described in Mayr to Dobzhansky, 11 June 1943 in Mayr/Dobzhansky Papers, folder “1937–1947.” Having been involved in several organizational launches, Huxley was no stranger to this sort of project.

final conference involving a symposium to be published in book form” remained a distant goal on his list of “concrete steps to be taken.” Simpson kept his emphasis on the *Bulletins*. Pessimistic, he only suggested, “The symposium planned as its final activity probably cannot be presented in 1945, but it is expected that this will be possible in 1946.”³⁴ As late as February 1946, when *Bulletin* 5 went to press, Princeton was not mentioned.

Plans for bicentennial celebrations circulating within Princeton University reached Jepsen early in 1945.³⁵ Ideas were not yet firm, but Jepsen knew his institution sought an international impression. Rumors suggested money would be plentiful. Administrators would be generous with resources. His role in the CCP aside, Jepsen was an certain participant in these celebrations. A conference on evolution was an obvious topic for him to organize.³⁶

Jepsen first proposed a connection between the Princeton bicentennial and the CCP in April 1945. In reply to a request from Simpson on the CCP’s future, Jepsen wrote, “... I have suggested that a symposium or panel or what not be held to consider our knowledge of genetics, paleontology, and evolution. The suggestion is being favorably considered and has almost limitless opportunity for expansion into biological and anthropological fields.” The value for the CCP was obvious, Jepsen noted. “Would this provide a satisfactory means of winding up or invigorating our committee?”³⁷

Jepsen’s suggestions arrived in Simpson’s post shortly after he had submitted the 1945 annual report to the NRC. It also arrived within days of a letter from Mayr on the future of the Committee. While Mayr agreed with Bucher and Dobzhansky in thinking a final meeting “still inopportune,” he suggested they should begin planning their final symposium.³⁸

34. “Report of the Committee on Common Problems of Genetics, Paleontology and Systematics,” 15 April 1945 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #2.”

35. Princeton University dates its founding to the 1746 and 1748 charters for the College of New Jersey (Leitch 1978). Conferences were only one aspect of their year-long celebration. The series *Bicentennial Conferences* reports on the conferences. An overview of the celebrations is provided by Princeton University (1946).

36. Part of Princeton’s class of 1927, Jepsen spent his career at Princeton. Trained by W. B. Scott and William John Sinclair, he moved through the ranks from instructor (1930). He also moved from curator of vertebrate paleontology (1935) to director (1940) of the Princeton Museum of Natural History (Gregory 1990). In 1945 Jepsen was considering leaving Princeton and was negotiating with Princeton management for promotion. Ultimately this led to his appointment as Sinclair Professor of Vertebrate Paleontology (1946). In part, Jepsen saw these celebrations as an opportunity to advance both himself and his museum within the Princeton community.

37. Jepsen to Simpson 3 April 1945 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #2.” Simpson was preparing the annual report for the NRC, see 15 April 1945 “Report of the Committee on Common Problems of Genetics, Paleontology and Systematics,” also in same folder, in which he simply noted the symposium cannot be held in 1945 but was expected for 1946.

38. Mayr to Simpson 4 April 1945 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #2.”

To no one's surprise, Simpson jumped at Jepsen's offer, calling the idea "an excellent one" and suggesting "of course, the Committee would be interested in this and also would provide a mechanism for obtaining and preparing speakers and data." Though he did not explain why, Simpson also noted he was "somewhat dubious as to whether this would be acceptable as the main or final product of the Committee."³⁹ Most likely, he wondered if the NRC would allow the Committee to claim a joint sponsor. But Princeton wanted a high profile for its bicentennial, and it was willing to generously underwrite any reasonable plan. Simpson suggested Jepsen make whatever progress he could with the idea. They could return to it if results were positive.

Jepsen's conference was not the only option for the CCP. In January 1946, nine months after Jepsen's suggestion about Princeton, Simpson consulted the NRC about how best to bring the Committee to a close.⁴⁰ He explained that "...with Mayr and Dobzhansky I have started work on a program" for a final conference.⁴¹ Holding the conference at Princeton remained one of two options. The other was "a conference of the New York Academy of Sciences, which has been running some very successful conferences in a variety of fields."⁴² Simpson asked about possible NRC objections to either co-sponsor.

As of January 1946, Simpson also had no clear publishing plan. He told the NRC that any conference volume would serve as "the chief permanent product of the Committee and in a sense its final report." That volume, he said, could be published as a special issue in a journal, such as *Lloydia*.⁴³ It also could be published in book form "such as in the Biological Symposia series of Cattell."⁴⁴ In the end, Simpson remained uncommitted.

With Princeton's deep pockets, Jepsen's proposal quickly became the favored option. Princeton ultimately provided over \$8,000 for their evolution conference. Simpson asked the NRC for \$4,000 in additional

39. Simpson to Jepsen 6 April 1945 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #2."

40. Simpson to Rubey 22 January 1946 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3."

41. This letter to Rubey corresponds with Simpson's writing of *Bulletin 5*, which makes no mention of Princeton but presents a discussion of possible conference topics. Simpson had been thinking of organizing these as early as Simpson to Mayr 6 December 1944 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1." This discussion carried through to the blank questionnaire, Appendix 6 here, circulated with *Bulletin 5*. It also shows a preoccupation with organizing the Society for the Study of Evolution and launching a new journal in evolutionary studies.

42. Simpson probably was thinking about symposia such as the 1942 symposium on criteria for genera, species and subspecies, in which he participated (Simpson 1943). Not coincidentally, Simpson's wife, Dr Anne Roe, served in several administrative capacities at the New York Academy of Science.

43. *Lloydia*, with Theodor Just as editor, published the symposium on historical patterns in *Drosophila* gene arrangements in Stebbins, et al. (1945).

44. Simpson did not know that Jepsen had previously interested Princeton University Press in any tangible output from the committee.

support but received only \$1,500.⁴⁵ This did not stop the CCP from slowly co-opting the conference: from their perspective, this was *their* conference and *their* agenda.

Ownership of the conference remained ambiguous through the first half of 1946. Joint planning was official by February 1946 (though Jepsen spoke of the CCP as “cooperating with” Princeton on the conference as late as July 1946).⁴⁶ Jepsen chaired a program committee that also included Mayr, Dobzhansky, and Kenneth Cooper (also at Princeton). For a time they referred to the project as the “Bicentennial and NRC Conference” and spoke of their institutions as “co-sponsors.” Interests clearly converged by April 1946, when Simpson announced the conference offered “a good way to wind up the Committee’s work.”⁴⁷ His 1946 annual report to the NRC made this plan explicit: “This Committee has been set up as a temporary stimulus rather than a permanent operating organization and it will end its work with the proposed conference and symposium.”⁴⁸ Committee members were informed of this plan through *Bulletin* 6, which was distributed in May.

During the summer of 1946, distinctions between the conference organizing committee and the CCP steering committee evaporated. By the end of the year, Simpson spoke about the Princeton conference as though it was always part of their plan. Though Jepsen (1948) drew a distinction between conference and Committee, the anthology of papers did not (Jepsen, Mayr, and Simpson 1949).⁴⁹

Princeton’s administration exerted its influence most strongly on the list of participants. They wanted an international impact and strongly

45. Arthur Bevan, “Report of Division of Geology and Geography to NRC Executive Board 20 December 1946,” in NAS Archives, folder “Geology and Geography. 1946. General.”

46. *Bulletin* 5, dated 5 February 1946, begins to outline a conference program but makes no mention of Princeton. The goal seems to be to decide on content and structure in the full knowledge that the location was still under negotiation. Simpson to “All Members of the Committee,” 15 February 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3” is Simpson’s first announcement to CCP members about locating the conference at Princeton. He describes the invitation to appear as “co-sponsors” of the conference and symposium volume, mentions NRC approval of the idea, and asks Committee members for their reaction. Chaney reported to Simpson that this would be discussed by the Western group at a meeting planned for 19 February (Chaney to Simpson 15 February 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3.” The conference planning in July is indicated by the invitation from Jepsen to Sonneborn 13 July 1946 in Sonneborn Papers.

47. Simpson to Rubey 1 April 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3.” Compare with correspondence in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3,” especially Simpson to Jepsen 6 February 1946 and Simpson to Jepsen 30 March 1946.

48. Appendix F, [CCP] Annual Report, April 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3.”

49. Organizers found it useful to keep the ownership of the Princeton conference polyvalent. The University could claim it as part of the bicentennial, and there was no point in challenging this view. Likewise, the Committee could claim it for themselves and represent it as their climactic moment. Key here is the convergence of interests.

encouraged Jepsen to invite leading researchers from Europe and the Soviet Union. This went far beyond the CCP's membership, but no one raised objections. This was a golden opportunity to re-establish contacts with colleagues and to meet those they did not know personally. Invitations to those in Axis countries proved difficult politically, especially for those in any way active in war work. Much discussion between the organizers took place over who might be invited and how their visits could be combined with other activities. Dobzhansky hoped to bring Dubinin, but fretted when the Soviets refused.⁵⁰

As is typical with projects of this ambition, the Princeton conference had its share of difficulties. Some were minor. For example, plans were drawn for a stenographic record of discussions, but proved too expensive. Instead, Jepsen circulated blank "discussion records" on which participants were asked to summarize their remarks.⁵¹

Other problems were major. Dobzhansky caused last-minute panic in October 1946 when he insisted on the participation of *Drosophila* geneticist, J.T. Patterson, in the program.⁵² After a flurry of activity in which Patterson declined participation, Dobzhansky resigned from his own role in the conference. Mayr and Simpson pressured Dobzhansky to change his mind, which he ultimately did.

Considerable momentum grew in the months leading up to Princeton. This helps account for the later sense that it offered a climatic moment. First, with visitors arriving from overseas and far away, there was the excitement for the conference itself.⁵³ Second, in the preceding au-

50. On Dubinin's invitation, see Dobzhansky to Dunn 23 January 1947 in Dunn Papers, folder "Dobzhansky, Theodosius 1946-1947." A list of those actually attending the conference is provided in "Appendix E / [CCP] / Annual Report, April 1947" in NAS Archives, folder "Geology and Geography. 1947. Meetings: Annual Meeting May."

51. The stenographic record was promised in Simpson to "members of the [CCP] and to other invited participants" 20 November 1946 with further discussion of expectations described in Jepsen to "Members of the Conference on Genetics, Paleontology, and Evolution" 4 December 1946, both in Sonneborn Papers. Examples of completed discussion sheets also are in Sonneborn Papers.

52. Dobzhansky described the problem as one of exclusion, "I have finally decided not to go to Princeton. There has been some sordid business on the part of one of the organizers (Cooper) excluding from the list of those invited to speak and even to attend people who do not please him and Sturtevant. Thus, Patterson and nobody of the Texas group are invited, and yet isn't [sic] true that the Texas group has done more about 'common problems' of evolution than any other geneticist or group of geneticists in the last half a dozen or more years? Since I happen to be a member of the committee I can not put myself in position of being responsible for these contemptible tricks." (Dobzhansky to Wright 18 October 1946 in Wright Papers, folder "Dobzhansky, Theodosius 1945-1949"; see also Dunn Papers, folder "Dobzhansky, Theodosius 1946-1947," and Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3a.") Dobzhansky reversed his decision several months later, after considerable efforts at persuasion (Dobzhansky to Wright 7 December 1946 in Wright Papers, folder "Dobzhansky, Theodosius 1945-1949"). As a consolation, Dobzhansky pressed hard to have J.T. Patterson made president of the Society for the Study of Evolution for 1947.

53. Jepsen planned a pre-conference circulation of remarks, providing a "preview" of the discussion (Jepsen to Wright 12 June 1946 and 30 Oct 1946 in Wright Papers, folder "Princeton Univ. Bicentennial"). A full set is included in Sonneborn Papers, with abstracts provided (in order of appearance on the program) by Knopf, Stern, Sturtevant, Romer, Chaney, Simpson, Stebbins, Mayr, and Wright.

tumn, Stebbins presented his Jesup lectures at Columbia University (Stebbins 1950). Third, the Princeton conference followed only a few days after the 1946 AAAS annual meeting in Boston. The Society for the Study of Evolution held its “first annual meeting” at the Boston meeting. In the business session Mayr announced the award of funding for their journal, *Evolution*, and recruiting for authors was well underway.⁵⁴ Most attending the Princeton meeting traveled directly from Boston. Finally, the conference had symbolic value for post-war reconstruction. Many of those in Princeton were seeing colleagues for the first time since the start of the war.⁵⁵ The conference offered a poignant symbol of survival and recovery, revived interest, and new directions.

At Princeton, the CCP held a formal meeting. No minutes were kept, and this seemed little more than a formality. For all intents and purposes, the CCP had ended.⁵⁶

After the conference, Simpson wrote to thank Princeton’s president, Harold Dodds.

The conference might have been considered a success even on the basis of our enjoyment of it, but it also had a more important success: it focused attention on some of the most essential of scientific problems, it pointed out ways for new and better attack on these problems by cooperative endeavor, and it inspired specialists in diverse fields to reorient their thinking and to plan work in new directions and on a broader basis. In these ways, the conference will have a permanent and constantly increasing effect on the progress and integration of the life sciences.⁵⁷

Soon thereafter some participants traveled to Paris for a similar conference. Simpson made sure the NRC noticed parallels.

You and the others there may be interested to hear of another development that shows how widespread is interest in the subject of the Committee and this Conference and how much our work has stimulated progress in this field. It has been decided to hold a colloquium on the same subject, “Genetics, Paleontology, and Evolution,”

54. The Society’s organizational meeting was held in March 1946 at the St. Louis AAAS meeting; its first regular annual meeting (complete with a program of events) was held in December 1946 at the Boston AAAS meeting (Cain 1994).

55. A conference photograph accompanies Jepsen (1948) and is reprinted in Cain (1993).

56. On the detailed plan for the conference, see Simpson to “Members” and “other invited participants” 20 November 1946 in Simpson Papers, folder “National Research Council.” Numerous programs survive of the conference, e.g., in Sonneborn Papers. Simpson’s copy includes annotations in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #4.”

57. Simpson to Dodds 9 January 1947 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #4.”

late in April under the sponsorship of the French Government, which, incidentally, will pay all expenses.⁵⁸

Production of the conference volume for Princeton was slow and tedious. Negotiations put control of the conference volume in the hands of the CCP, rather than Princeton or the NAS. A basic plan was in place as early as November 1946, with Simpson stressing to authors how papers “must be definitely pertinent to the subject of the symposium: evolution as a synthesis of studies in genetics, paleontology, and systematics.”⁵⁹ Princeton subsidized publication through its university press. Reprints of chapters were not issued to authors, as Jepsen explained “because the intended effect of the volume is to direct attention to the synthesis and integration of the material rather than to fractional parts of it.”⁶⁰ The NRC agreed to divert any profits from the sale of the conference volume (after repaying the NRC’s subsidy) to the new Society for the Study of Evolution.⁶¹

With the publication of the conference volume Simpson requested the Committee be discharged. “Continued activity in the field of the Committee, on a broader and permanent basis,” he explained, “is provided for by the Society for the Study of Evolution.”⁶² The formal approval of this request brought the CCP to a close.

Simpson’s Next NRC Committee

Least well known of the projects growing from the CCP was work done by Simpson during 1946–1947 to create the “Committee on the Application of Biological Data and Methods to Geological Problems” (CAB). As Simpson explained to a colleague, the NRC “has asked me to organize” this committee as part of a “general program involving a sort of cross-fertilization between the sciences...”⁶³ With the CCP and other

58. Simpson to Margaret Johnson 8 Nov 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3.” Notes on the Paris conference are in Simpson Papers, folder “Colloquium on Paleontology, Paris, 1947.” Conference papers are published in Arambourg, et al. (1950).

59. Simpson to “members of the [CCP]” 20 November 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #3a.” Simpson wanted others to undertake this work, asking Jepsen, Mayr, and Dobzhansky to edit the symposium volume. “Will you accept this additional and final duty for the NRC Committee?” Simpson to Jepsen, Mayr and Dobzhansky 18 November 1946 in Simpson Papers, same folder; and Simpson to Jepsen 26 November 1946 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) conference expenses, 1946–1947.”

60. Jepsen to authors 27 May 1948 in Sonneborn Papers.

61. Relevant correspondence is located in NAS Archives, folder “Biology and Agriculture. 1948. General.”

62. Annual Report of the [CCP], April 1949 in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #5a.” Related correspondence is in NAS Archives, folder “Biology and Agriculture. 1949. General.”

63. On the CAB, see Simpson Papers, folder “National Research Council (Committee on the Application of Biological Methods and Data to Geological Problems),” especially Simpson to Ralph Chaney 22 May 1946 and Simpson’s draft proposal for the CAB, 27 June 1946. This work was undertaken in cooperation with Schairer. See also NAS Archives, folder “Geology and Geography. 1946. General.”

projects as exemplars, the overall objective for the CAB was to focus collaborative attention on geological researches “that require or could profitably use biological methods and data.”

The purpose will be to define problems of this type, to bring together biologists and geologists who may be able to combine efforts on the problems, to summarize what has been done on them, and to suggest what more could profitably be done on them in the near future.⁶⁴

Simpson committed considerable time and effort in 1946–1947 to this project.⁶⁵ The CAB involved at least seven subcommittees:

- applying biochemistry to geochemistry
- biochemistry to petrology
- microbiology to petrology
- statistics to petrology
- biology to geochronology
- biogeography to paleoclimatology
- biogeography to paleogeography⁶⁶

Simpson planned additional subcommittees, too: botany to physiography, ecology to paleogeography and petrology, and evolution to historical geography.⁶⁷ However, these were cancelled for lack of willing personnel to drive the work forward. In conjunction with the CAB, the NRC’s Division of Geology and Geography also sponsored a “Committee on the Application of Physics and Chemistry to Geological Problems.” Its design was equally expansive.⁶⁸

The CAB collapsed underneath its own weight. Acknowledging his over-ambitiousness, Simpson resigned the CAB chair in 1947. The NRC replaced him with G. Evelyn Hutchinson.⁶⁹ Even so, the CAB developed few plans for action.⁷⁰ Without comment, the NRC dissolved the CAB at the end of its 1948–1949 fiscal year.

64. Simpson’s draft proposal for the CAB, 27 June 1946, Simpson, folder “National Research Council (Committee on the Application of Biological Methods and Data to Geological Problems).”

65. *Report of the National Academy of Sciences. National Research Council. Fiscal Year 1946–1947*, p. 60 in NAS Archives.

66. Bevan to Simpson 31 July 1946 in NAS Archives, folder “Geology and Geography. 1946. General.”

67. Simpson “proposal for organization” circa 27 June 1946 in Simpson Papers, folder “National Research Council (Committee on the Application of Biological Data and Methods to Geological Problems).”

68. Schairer to Bevan 17 June 1946 in NAS Archives, folder “Geology and Geography. 1946. General.”

69. Simpson complained his workload at the American Museum was too great for him to continue with the CAB in Simpson to Bevan, 3 March 1947 in Simpson Papers, folder “National Research Council (Committee on the Application of Biological Data and Methods to Geological Problems).”

70. See reports in NAS archives, folders “Geology and Geography. 1948. Meetings: Annual Meeting April” and “Geology and Geography. 1949. Meetings: Annual Meeting April.” See also Delo to Bronk 16 Sept 1949 in NAS Archives, folder “Biology and Agriculture. 1949. General.”

■ 5. Conclusion

When telling his version of the history of evolutionary studies—as in his Foreword to the present volume—Mayr stressed the value of systematics in linking the two other groups of evolutionists. This presented but one perspective found in the overall coalition supporting the CCP (Cain 2003). Paleontologists told the history of the CCP with important differences. So did those in the West Coast group. So did those watching from outside. There is historical value on this variety of perspectives.

Mayr's representation of the CCP as a progressive development in split-mending and gap-filling allowed him to position the CCP as a natural and unproblematic step in the progressive development of a discipline. Be that as it may, his presentation underplays important turns in the CCP's overall history and selectively highlights some outcomes over others. Significantly it poorly captures Mayr's own role in shaping the intellectual and social flavor of the committee as it evolved. His was hard work: in no way simply natural and unproblematic. Others worked hard too, and their contributions need closer study. Though Mayr's recollections have influenced several generations of historians, returning to the primary sources of the period offers the only way to balance the insights of Mayr's recollections with the voices of others long left to the silence of the past.

The CCP marks a key transition in American evolutionary studies. It was launched with relatively modest goals by paleontologists anxious to modernize their discipline and improve their status as working biologists. Owing to changes in the Committee's leadership, this agenda was subordinated by a more general interest in community building within evolutionary studies and other modernizing agendas. This focused attention on common interests related to evolutionary processes and mechanisms. The Committee's intellectual activity is best captured in its one 1943 *Report* and four 1944 *Bulletins*. By the end of 1944, the Committee's leadership felt confident enough to expand this enterprise. They transformed the temporary Committee mechanism into a stand-alone professional society with its own journal. They co-opted Princeton's bicentennial to create a climactic moment. They also used their considerable momentum in other ways to promote the view that a revolution in evolutionary studies was underway and they were at its center.

Seen within the overall sweep of organizational initiatives in the synthesis period, the CCP represents a fine example of a "transition community," which Bruffee (1993) proposed to identify early stages in the origin of new research communities and new disciplines. It provided a relatively forgiving intellectual space where researchers could admit their lack of expertise, acquire new skills, and test them within a supportive environment. The Committee also nicely illustrates how an

interdisciplinary “trading zone” operates, especially in the way actors create infrastructure both to facilitate trading and to manage the overall process to best suit their own objectives (Star and Griesemer 1989; Galison 1999).

The CCP was by no means homogenous. Eastern and Western groups showed distinctly different characters. The need for tying evolutionary disciplines together was strong in zoology, far less so in botany as integrative work already was well underway. The same could be said about needs in institutions on the East Coast compared with those in the West. Individuals representing paleontology (especially paleozoology) felt far different needs compared with those representing genetics or systematics. As a case study, the CCP demonstrates the value of a polyvalent approach to studying interdisciplinary projects (Cain 2003).

The history of the CCP also is a history of the rise of Ernst Mayr to a central role within the evolutionary studies community. With Simpson and Dobzhansky away, the CCP unexpectedly provided him an opportunity at the helm. He took great advantage of the moment: pressing for results within the Eastern group, organizing the *Bulletins*, and exploiting the momentum for further gain. He had been waiting more than a decade for a chance to promote reforms to zoology. His success within the CCP proved to others that he had the energy and determination to drive their common agenda ahead. If any moment must be chosen as critical for his transition to a leadership role, it is within the CCP. Building on the success of his book (Mayr 1942), Mayr demonstrated his capacity and perseverance at the national level. The rest of his success was by no means certain, but the CCP gave him the confidence and the credibility on which the rest could build.

As with Mayr, so too for the New York circle as a whole. The CCP mechanism gave a focus to their overlapping interests, like that already accomplished in the Western group. It also provided a legitimating device for them within the professional infrastructure of biology as it was practiced on America's East Coast. Members of the New York circle often disagreed on particulars, but they shared similar visions regarding the potential of their Committee. Another result of their cooperation was the bolstering of their own status as inter-disciplinarians to a level comparable with other innovative researchers in evolutionary studies of the period. Each in the circle now could claim status comparable to highly respected peers, such as Alfred Emerson, Carl Hubbs, and Ernst Babcock. This effort proved more successful than they might have anticipated. By the Committee's closure, the New York circle was squarely at the helm of professional infrastructure in American evolutionary studies.

TABLE 1

Committee on Common Problems in Genetics and Paleontology, 2 October 1943.

With notes on changes during the Committee's lifespan. Source: *Report of Meetings*, October, 1943. Modified from the original to complete names.

George Gaylord Simpson, Chairman
Walter Hermann Bucher, Acting Chairman

	Section on Paleontology	Section on Genetics
	Glenn L. Jepsen chair of section	Theodosius Dobzhansky chair of section Ernst Mayr ⁷¹ acting chair of section
Eastern Group	Section on Paleontology	Section on Genetics⁷²
	Walter Hermann Bucher ⁷³ chair of Eastern Group Kenneth Edward Caster Edwin Harris Colbert Gustav Arthur Cooper Carl Owen Dunbar Glenn Lowell Jepsen Bryan Patterson ⁷⁴ Fred B. Phleger Alfred Sherwood Romer George Gaylord Simpson Horace Elmer Wood, 2nd	Kenneth Willard Cooper Milislav Demerec Theodosius Dobzhansky Myron Gordon Ernst Mayr Hermann Joseph Muller Warren Poppino Spencer Curt Stern Sewall Wright
Western Group	Section on Paleontology	Section on Genetics⁷⁵
	Daniel Isaac Axelrod Ralph Works Chaney Bruce Lawrence Clark ⁷⁶ Maxim Konradovich Elias Herbert Louis Mason Chester Stock	Edgar Anderson Ernest Brown Babcock, chair of Western Group Carl Clawson Epling George Ledyard Stebbins, Jr., vice-chair of Western Group

71. When systematics is added to the Committee's remit, Mayr becomes "Chairman, Section on Systematics," as in Bevan to "Members of the Committee..." 31 July 1946 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3a."

72. Leslie Dunn was invited to join the Eastern geneticists, but declined.

73. When Bucher left the Chairmanship of the Division of Geology and Geography, he asked to be relieved of this duty, see Bevan to "Members of the Committee..." 31 July 1946 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3a."

74. Bryan Patterson served in the U. S. Army from October 1943, returning in mid 1945. His details were reported in Society of Vertebrate Paleontology News Bulletin 14 (30 April 1945): 8–9; and 15 (22 September 1945): 13.

75. Jens Clausen was invited to join the Western geneticists, but declined.

76. Bruce Lawrence Clark died 23 September 1945, for a memorial, see Camp (1947).

TABLE 2	
Publications of the Committee on Common Problems in Genetics and Paleontology, 1943–1949.	
Reports	Report of Meetings of the Committee, October 1943, containing: summary of Berkeley meeting of Western Group, June 14–16, 1943 summary of New York Meeting of Eastern Group, July 24–25, 1943 abstracts of papers presented at New York meeting
Bulletins	no. 1 (28 pp., May 15, 1944, edited by Mayr) no. 2 (35 pp., June 26, 1944, edited by Mayr) no. 3 (27 pp., September 25, 1944 , edited by Mayr) no. 4 (26 pp., November 13, 1944 , edited by Mayr) no. 5 (8 pp., February 5, 1946, written and edited by Simpson) no. 6 (9 pp., May 5, 1946, written and edited by Simpson)
Conference Reports	Glenn L. Jepsen. 1948. "Genetics, Paleontology, and Evolution," <i>Princeton University Bicentennial Conference</i> , series 2, conference 3. Glenn L. Jepsen, Ernst Mayr, and George G. Simpson (eds.). 1949. <i>Genetics, Paleontology, and Evolution: Proceedings of Princeton Conference (January 1947)</i> . Princeton: Princeton University Press.

TABLE 3

Subject Threads in *Bulletins* 1–4.

This table represents the subject threads of the correspondence in *Bulletins* 1–4, as dialogue developed. Correspondence is nested according to replies. For instance, Chaney's 29 March letter to Dobzhansky replies to Dobzhansky's from 5 February. (All correspondence took place in 1944.) All correspondence at the same hierarchical level replies to same letter. For instance, letters 1.a.i. and 1.a.ii. reply to 1.a. One letter is listed twice because the author explicitly draws two connections. *Bulletin* numbers are listed in [] brackets.

1. Dobzhansky to Chaney, 5 February 1944 [1]
 - a. Chaney to Dobzhansky, 29 March 1944 [1]
 - i. Dobzhansky to Chaney, 14 April 1944 [1]
 - a. Stebbins to Dobzhansky, 1 May 1944 [1]
 - i. Stebbins to Colbert, 8 June 1944 [3]
 - b. Epling to Dobzhansky, 14 May 1944 [2]
 - c. Epling to Dobzhansky, 18 May 1944 [2]
 - d. Elias to Dobzhansky, 28 June 1944 [4]
 - i. Babcock to Elias, 18 July 1944 [4]
 - ii. Babcock to Dobzhansky, 28 April 1944 [1]
2. Mayr to Colbert, 7 March 1944 [1]
 - a. Colbert to Mayr, 20 March 1944 [1]
 - i. Stebbins to Colbert, 8 June 1944 [3]
 - b. Wright to Mayr, 1 June 1944 [2]
3. Mayr to Stern, 7 March 1944 [2]
 - a. Stern to Mayr, 13 May 1944 [2]
 - i. Dobzhansky to Stern 19 August 1944 [3]
4. Jepsen to Caster, 2 May 1944 [2]
 - a. Caster to Jepsen, 9 May 1944 [2]
5. Jepsen to Mayr, 4 May 1944 [2]
 - a. Mayr to Jepsen, 22 May 1944 [2]
6. Babcock to Mason, 31 July 1944 [3]
7. Stebbins to Dobzhansky, 28 July 1944 [3]
 - a. Dobzhansky to Stebbins 18 August 1944 [3]
8. Stebbins to Mayr 25 July 1944 [4]
 - a. Mayr to Epling 28 July 1944 [4]
 - i. Colbert to Mayr, 29 August 1944 [4]
 - ii. Stebbins to Mayr, 1 September 1944 [4]
 - a. Mayr to Stebbins, 8 September 1944 [4]

EDITORIAL NOTES

Joe Cain

Source texts for the *Report of Meetings* and *Bulletins* are located in Simpson Papers, folder: “National Research Council (Committee on Common Problems of Genetics, Paleontology and Evolution) #6.” A duplicate set is located in NAS Archives, folders “Geology and Geography. 1944. Committee on Common Problems of Genetics, Paleontology and Systematics” (*Bulletins* 1 through 4) and “Geology and Geography. 1946. Committee on Common Problems of Genetics, Paleontology and Systematics. It w Division of Biology and Agriculture” (*Bulletins* 5 and 6). The source texts used here were as distributed to Committee members and sponsoring division chairs of the National Research Council. Sources for texts used in Appendices and elsewhere are specified in editorial footnotes.

The inscriptional history for documents incorporated into the *Report* and *Bulletins* is difficult to trace. The original documents used for compiling the *Report* are lost. Most original letters reproduced in the *Bulletins* are lost, too. Those that have been located are identified in editorial footnotes. Without many originals, the extent of editorial intervention by the *Report*’s producer(s) or by Mayr while he compiled *Bulletins* 1 through 4 is difficult to assess. Readers might presume Mayr followed the procedure described at the start of *Bulletin* 1. Some documents were assembled for a fifth bulletin of correspondence, but Simpson changed the purpose of *Bulletin* 5, and those letters did not appear in CCP circulars. The contents of that fifth issue of correspondence is unknown.

The *Report* and *Bulletins* were printed on 8½ x 11-inch white paper. The source text was typed in double-spaced lines, single-column format, and was printed on both sides of the paper. Circulating copies were produced by stencil and mimeograph technology. In a 1994 interview, Mayr reported his wife, Gretel, typed stencils for *Bulletins* 1 through 4. Presumably Simpson’s secretary typed the stencils for *Bulletins* 5 and 6. It’s not clear where the mimeographing occurred, or who posted the circulating material. Certainly, postings came either from Mayr’s, then Simpson’s, department at the American Museum of Natural History in New York, or from NAS offices in Washington, DC.

The aim of the present edition is a letter-perfect transcription of the original source documents following Kline (1998: 161–164). Nomenclature has not been updated. Spelling, grammar, and stylistic consistency remains as in the original. Underlining in the source texts is replaced by italics here. Underlining here denotes additional emphasis made by authors. All ellipses are in the original except when placed in [] brackets.

A limited number of editorial interventions appear in the original texts. Presumably these were inserted by Mayr, then Simpson. These interventions are identified in Cain's footnotes. Annotations in handwriting on the original documents are rare. These also are noted in Cain's footnotes. Because the source documents used for this edition are relatively free of annotations and revisions, no textual record has been prepared. Except where noted, all footnotes are editorial interpolations or annotations by Cain.

Cain's editorial interventions follow these conventions:

- [] editorial interpolations or expansions
- / line break, except with "and/or" or when used in footnotes.
- [¶?] presence of a new paragraph suspected but not clearly demarcated, usually coincidental with page transitions.

Pagination is indicated by [] brackets with the following conventions:

- [x|y] page transition in the source document, from page x to page y.
 - [x|y*] page transition in the source document, from page x to page y, occurs within a word. To preserve clarity, the marker is shifted to the end of the transitional word.
- "cover page" denotes an unnumbered cover page.

Page numbers "cover page," "i" and "1" are added by Cain. Line breaks are not preserved from the original source. Paragraph breaks follow the original, except where noted.

Many publications are cited in the source documents. The completeness and the presentation styles vary widely. In some cases the original style of citation is preserved. In most cases, however, editorial notes by Cain replace incomplete or ambiguous citations. These notes correspond to citations in the bibliography.

Transcription has been verified by two complete and independent rounds of visual collation followed by proofreading of samples from each document as recommended by Kline (1998: 204–207).

CALENDAR OF CORRESPONDENCE

This calendar lists correspondence that appeared in *Bulletins* 1–4. Subjects for *Bulletins* 2–3 were provided by Mayr in the original issues. Cain adds subjects for *Bulletins* 1 and 4. *Bulletins* 5 and 6 contained no correspondence.

1. Bulletin 1: May 15, 1944

date (1944):	from:	to:	subject:
5 February	Dobzhansky	Chaney	problems determining species status using paleobotanical material, taxonomic practices in paleobotany
29 March	Chaney	Dobzhansky	reply
14 April	Dobzhansky	Chaney	botanical evidence for evolutionary changes during the Tertiary
28 April	Babcock	Dobzhansky	reply to 14 April letter. Summary of <i>Crepis</i> research
1 May	Stebbins	Dobzhansky	reply to 14 April letter. Evolutionary patterns and rates in paleobotany and botany
7 March	Mayr	Colbert	rates of evolution in vertebrates and questions of causal relationships, e.g., environmental changes, role of population density
20 March	Colbert	Mayr	reply

2. Bulletin 2: June 26, 1944

date (1944):	from:	to:	subject:
7 March	Mayr	Stern	genetic differences between individuals, populations, and species. On possible genetic devices of sympatric speciation
13 May	Stern	Mayr	same
2 May	Jepsen	Caster	correlation between breaks in phylogenetic series and gaps in fossil evidence
9 May	Caster	Jepsen	same
4 May	Jepsen	Mayr	concepts and terminology of vertical subspecies and species
22 May	Mayr	Jepsen	same
14 May	Epling	Dobzhansky	rate of evolution in plants
18 May	Epling	Dobzhansky	existence and relative importance of polytypic species among plants
1 June	Wright	Mayr	correlation between population structure and rate of evolution

Bulletin 3: September 25, 1944

date (1944):	from:	to:	subject:
8 June	Stebbins	Colbert	evolutionary factors and the fossil evidence
31 July	Babcock	Mason	origin of the genus <i>Pinus</i>
28 July	Stebbins	Dobzhansky	relative frequency of visible as compared to lethal mutations in <i>Drosophila</i>
18 August	Dobzhansky	Stebbins	same
no date	Spencer		comparative mutation rates in <i>Drosophila</i>
			species (reprinted manuscript)
19 August	Dobzhansky	Stern	occurrence of sympatric speciation

Bulletin 4: November 13, 1944

date (1944):	from:	to:	subject:
25 July	Stebbins	Mayr	antiquity of disjunctive groups, plants and <i>Drosophila</i>
28 July	Mayr	Epling	evidence on age of discontinuities in distribution of <i>Drosophila</i>
29 August	Colbert	Mayr	climatic changes in the Pleistocene
1 September	Stebbins	Mayr	reply to Mayr's criticisms of Epling's interpretation of <i>Drosophila</i> distribution
8 September	Mayr	Stebbins	further discussion of <i>Drosophila</i> distribution
28 June	Elias	Dobzhansky	rates of evolution in plants
18 July	Babcock	Elias	evolutionary rates in <i>Crepis</i>

REPORT OF MEETINGS OF THE COMMITTEE ON COMMON PROBLEMS OF GENETICS AND PALEONTOLOGY

(Joint Committee of the Divisions of Geology
and Geography, and Biology and Agriculture)

Part I Berkeley meeting of Western Group, June 14–16, 1943

Part II New York meeting of Eastern Group, July 24–25, 1943

Part III Abstracts of papers presented at New York meeting

October, 1943

[cover page |i]

[Page i consists of a roster of the Committee as of October 2, 1943. This is reproduced in Table 1 in Cain's historical introduction.]

[i1]

Part I / Report of the Meeting of the Western Group / of the / Committee on Common Problems of Genetics and Paleontology / National Research Council / June 14–16, 1943

The group met first on June 14, at 1:30 P.M., in Room 310 Hearst Mining Building, University of California, Berkeley. The following members were present: E. Anderson, E.B. Babcock, R.W. Chaney, M.K. Elias, C. C. Epling, H. L. Mason, and G.L. Stebbins, Jr.⁷⁷ A discussion on "Tertiary Ancestors of Tropical Floras" was led by Chaney. The following is an abstract of his remarks.

[Abstract begins⁷⁸] While the determination of the taxonomic status of Tertiary leaves is based primarily upon comparisons with the leaves of living species, it is desirable to emphasize that fossil leaves in themselves may indicate the general environment under which plants of the past have lived.

Published lists of Eocene floras from the western United States include numerous species, and in some cases several

77. Sewall Wright expected to attend the Western Group's meeting and agreed to deliver a fifth session on "rates of evolution in relation to population dynamics." This session did not occur, and Wright was not listed as a participant. On the plan, see 1 June 1943 revised "Appendix N: Report of the Committee of Common Problems of Genetics and Paleontology" in NAS Archives, folder "Geology and Geography. 1943. Committee on Common Problems of Genetics and Paleontology." Also see correspondence with Edgar Anderson in Wright Papers, folder "Anderson, Edgar 1932–1960." Dobzhansky also invited Wright to the Eastern Group's meeting, but he declined citing prior commitments in California. See Wright Papers, folders "Dobzhansky, Th. 1943–1944" and "Stebbins, G. Ledyard, Jr."

78. No evidence speaks to the question of authorship for these abstracts. It might have been the presenters themselves or Stebbins as recorder. These abstracts are not indented in the original.

genera, in such families as the Euphorbiaceae, Lauraceae, Leguminosae, and Moraceae. Trees of these are now characteristic of low latitudes, and it may be assumed that if our fossil species are properly identified, they were inhabitants of a subtropical environment. But even if errors in identification are involved, the leaves of most of these Eocene species bear the mark of a climate with high temperature and abundant rainfall. Their size, texture, margin, and nervation characters seem to relate them not only to living plants of low latitudes, but to living conditions of the tropics. Greater size and thicker texture may be noted in comparison with the leaves of Middle Tertiary floras, whose common members fall in such typically temperate families as the Betulaceae, Fagaceae, and Salicaceae. Margins of the Eocene leaves are more regularly entire, and their nervation is commonly camptodrome rather than craspedodrome. In the percurrent rather than reticulate character of the finer nervation, and in the trend of these finer nerves more nearly at right angles to the major axis of the leaf, further resemblances to modern leaves of low latitudes are indicated.

Since Tertiary leaves may be assigned to modern families and genera both on the basis of resemblances to living plants, and of morphological characters consistent with the modern habitats of these plants, we conclude that the correctness of our identifications and of our conclusions regarding their environments is reasonably well established. [Abstract ends]

Discussion centered about the morphogenetic interpretation of the differences between tropical or subtropical and temperate types of leaves, and the effect which the selective action of the environment might have on producing the differences between them. Stebbins pointed out that some of the characteristics of leaves of temperate species, particularly the serrate margins and the craspedodrome venation, might be associated with their folded condition in the bud during late winter and early spring, i.e. with the plicate type of vernation. Both this type of vernation and the thin texture [1|2] of the leaf make possible the rapid expansion of the photosynthetic surface at the beginning of active growth after the winter dormancy. They are thus adaptations to the seasonal cycle present in temperate regions. On the other hand, the margin and venation of tropical leaves are associated with simpler types of vernation, in which expansion of the leaf surface is slower, an adaptation to the less marked seasonal rhythm characteristic of the tropics. The large size and thick texture would produce the maximum amount of photosynthetic activity, which would be an advantage under the optimum growing conditions of moist tropical regions.

The second discussion, held at 9:30 A.M. June 15, was led by Babcock, on the subject of Tertiary plant migration in Eurasia, with special reference to the holarctic distribution of *Crepis*. The following is an abstract of his remarks.

[Abstract begins] 1) The antiquity of *Crepis* is indicated by its holarctic distribution. The nunatak areas of *C. nana* and the nature and distribution of the polyploid American species require a Tertiary origin. Distributional evidence in Eurasia agrees with this. The argument is clinched by the existence of fossil seeds of three primitive *Crepis* species from Middle and Upper Pliocene beds in western Europe. 2) Phylogeny in *Crepis* is based on comparative morphology. The nearly 200 species have been arranged in 27 sections; these are assembled into 3 groups, primitive, intermediate, and advanced. The evidence from chromosome number and morphology and from genetics is generally consistent with this classification. The genus as a whole is monophyletic and had one center of origin. 3) Geographic distribution of most of the related genera of the various sections of *Crepis*, and of primitive and advanced endemics in this genus, all point to north Central Asia as the most probable center of origin of *Crepis*. To explain the present distribution of *Crepis* it is necessary to assume four migration routes, radiating from the center of origin: *a*, northeasterly across Beringia into North America; *b*, southeasterly into southwestern China, eastern Tibet and Annam; *c*, south into the western Himalayas and southwesterly into Iran where the route forked, one branch going through Asia Minor into southern Europe and the other, through Arabia into tropical Africa; *d*, westerly over the south end of the Urals into eastern Europe. 4) Strong positive correlation of the above evidence on *Crepis* with fossil and present-day floristic evidence is abundantly indicated; but the evidence from *Crepis* alone is sufficiently convincing to warrant its consideration as supplementary to, rather than requiring the corroboration of, any other evidence. [Abstract ends]

Discussion centered about the relation between the migration pattern of *Crepis* and that of the woody genera of which more abundant fossil remains are available. Chaney pointed out that the main southwesterly path of migration postulated for *Crepis* could be considered as a modification of the general north-south trend recognized from fossil evidence as characteristic of the floras of later Tertiary time. [2][3]

In the third discussion, held at 1:30 P.M., June 15, Mason introduced the subject of the relation between populations of plant species in the Pliocene and Pleistocene epochs and modern populations of the same

species with an account of the evidence from certain species of *Pinus* native to California. His remarks may be summarized as follows:

[Abstract begins] An example of natural genetic processes in the development of present day floras is afforded by the fossil and recent history of the Insignes section of the genus *Pinus*. This section is represented in the California flora by four species, *P. radiata*, *P. attenuata*, *P. muricata*, *P. remorata*. All of these are recorded in the literature from the Pleistocene and *P. radiata* and *P. muricata* are known down into the Pliocene. All are discontinuous in the modern floras, and give evidence of being relicts.

Pinus muricata is a somewhat polymorphic type ranging discontinuously from Crescent City in Del Norte County, California, to Point San Quentin in Baja California. There are four major breaks in its range. In the north it is a massive tree with large trunk and dark green foliage, occurring on deep and oftentimes wet soil but extending into pine barrens. In the south it is a small tree with slightly glaucous foliage on shaly ridges suggestive of pine barrens conditions. The growth form and aspect of the two are quite different and may warrant taxonomic separation. The cone scales of the northern type, although well developed, are not so conspicuously so as those of the southern type. Both forms are represented in the Pleistocene fossil record and this character seems to have been differentiated at that time as well as today.

Pinus remorata is an insular endemic confined to Santa Cruz, Santa Rosa, Guadalupe and Cedros islands. It differs from *P. muricata* in having symmetrical cones, smooth umbos when mature, thicker needles, and in some of the anatomical details of the needles.

On Santa Cruz Island there is abundant evidence that the two species cross, since much intergradation exists. On La Purisima Ridge of the mainland, a colony of intermediate types occurs. Search of the entire population has failed to yield a single positive *P. remorata*, but many stages of intermediacy may be found.

In the Pleistocene Santa Cruz Island flora Chaney and Mason reported *Pinus remorata*. The specimens were numerous, all essentially uniform, and were clear cut examples of typical *P. remorata*. In the several lenses investigated no specimens of *P. muricata* were discovered. All lenses contained *P. remorata*.

At Carpinteria across the Santa Barbara Channel were found in Pleistocene deposits *P. radiata* and *P. muricata* in great abundance, and two imperfect cones of *P. remorata*. Today at

Carpinteria none of these species occur. The Purisima Ridge locality to the north is separated from this region by the Santa Ynez range of mountains. [3|4]

What seems to be happening is the genetic submergence of *P. remorata* by the ecologically more vigorous *P. muricata* through a process of gene infiltration. The process has gone farthest at Purisima Ridge, is well under way on Santa Cruz and Santa Rosa islands, but was not evident on Santa Cruz island during the Pleistocene. *Pinus remorata* comes true from seed. [Carl Brandt] Wolf at Rancho Santa Ana Botanic Garden has a plantation of several hundred individuals all essentially alike.

An experiment was being devised to be set up at the Institute of Forest Genetics to study the problem and the seed was collected, but the project was temporarily discontinued owing to the war effort. [Abstract ends]

Discussion centered about the value of careful analyses of variability in the populations under discussion. It was generally agreed that these pines provide unique material, offering an unparalleled opportunity for the study of the dynamics of evolution in plant populations. The continuation of this project was strongly recommended as soon as conditions permit. A similar but more complex situation was described by Mason in certain species of the genus *Ceanothus*, section *Cerastes*, occurring in the region north of San Francisco Bay. In this group the number of populations and of entities involved is larger, and there is evidence of present and past hybridization, but the fossil material available is very scanty.

In a continuation of this discussion, Epling produced evidence from present distribution that certain inversion types in the third chromosome of *Drosophila pseudo-obscura*, i.e. Santa Cruz and some of its derivatives, attained the limits of their present range in the early part of the Tertiary period, and have since been eliminated from northern Mexico and parts of the southwestern United States. It seems likely therefore that in *Drosophila* as in *Pinus* the evolution of certain species during the latter half of the Tertiary period has consisted largely in the change of frequency of certain genetic types in the populations.

The final discussion, on June 16, at 9:30 A.M., was led by Elias. An abstract of his remarks on "Orthogenesis, the size factor, and other major evolutionary trends in plants" follows.

[Abstract begins] Accurate information on the position of fossil organisms in the stratigraphic succession of rock formations is essential in the study of orthogenesis, that is continuous evolution. Stratigraphic errors of various magnitude crept in many schemes of evolution of plants and animals in the past and weeding out of these errors is one of the urgent problems today.

Only a few reliable examples of orthogenetic series illustrating the course of evolution in some late Paleozoic and Tertiary terrestrial plants may be now demonstrated. Examples of *Sphenophyllum* from the late Pennsylvanian and early Permian of the Northern Midcontinent demonstrate gradual development of anisophylly and perfection of leaf mosaic in the stock adapted to life in diffused light in the shade of the forest. A fern, *Pecopteris vestita*, in [4|5] the same forest, shows gradual increase in the size of its fronds.

Seeds of Water-Soldier (*Stratiotis* [*sic*: *Stratiotes*]), studied by Chandler, demonstrate gradual evolution from the Eocene to the present in the change from coarsely corrugated and short to smooth and elongated seeds. Seeds of *Stipeae* in the Miocene and Pliocene terrestrial rocks of Nebraska show the following evolutionary trends: increase in size (but in a few cases also diminution in size); closing of lemma by overlap of the edges, or by their interlocking in the grooved palea; reduction to nearly complete suppression of palea; reduction of callus. [Abstract ends]

In the discussion, Anderson pointed out the essential importance for all demonstrations of orthogenetic trends of statistical data on the amount of variability in the fossil material of any given age. In connection with the *Stipeae*, Stebbins pointed out the fact that the range of variation found in the entire series of fossils from the Great Plains is exceeded by that known in living species of the tribe, if all of its species throughout the world are taken into account.

Preceding this last discussion, the following business was transacted. As permanent chairman of the western group, E.B. Babcock was unanimously elected, with G.L. Stebbins Jr., as vice chairman. As a new member of the committee, the selection of Bruce L. Clark, Division of Paleontology, University of California, Berkeley, was unanimously recommended. It was resolved that another meeting of the western group should be held in about a year's time if practicable, the time and place being decided upon at a future date. A meeting of the entire committee was recommended as soon as conditions permit.

For the concluding meeting, the group was entertained by Dr. Chaney at his home. He demonstrated his garden, in which he has assembled the nearest living relatives of the Tertiary and Cretaceous plant formations of Western North America. The meetings were voted an unqualified success, and gratitude was expressed to the National Research Council for making them possible.

G. Ledyard Stebbins Jr.,
Acting Chairman [5|6]

Part II / Report on the Meeting of the Eastern Group / of the / Committee on Common Problems of Genetics and Paleontology / National Research Council / July 24–25, 1943

The group assembled in the Sportsmen's room of the American Museum of Natural History at 9 A.M., on Saturday, July 24, and soon after started on the program which had been organized by the section chairmen, Drs. Jepsen and Mayr.⁷⁹ After a noon recess, the meeting continued to well after 5 P.M. The program was continued on the next day and was brought to a close about 6 P.M.

The following members were present:

(a) Genetics and allied fields of Biology: K. W. Cooper, M. Demerec, Myron Gordon, E. Mayr, H. J. Muller, W. P. Spencer,⁸⁰ Curt Stern.

(b) Paleozoology and allied fields of Geology: W.H. Bucher, K. E. Caster, E. H. Colbert, G. D. [*sic*: L.] Jepsen, Bryan Patterson, F. B. Phleger, A. S. Romer.

In addition to the official members, C. O. Dunbar⁸¹ and a number of other invited guests were present at the meeting.⁸²

The meeting was opened by E. Mayr with a welcome from the Director of the Museum [Albert Parr] who could not be present personally. W. H. Bucher presented a brief summary of the chairmanship of the Division of Geology and Geography of the National Research Council. The meeting was then taken over by the section chairmen, Glenn Jepsen and E. Mayr, who took turns presiding over the four half-days that were devoted to scientific papers, each of which was followed by prolonged, active discussions.

A. The papers presented.

The papers were grouped under four main topics as follows:

I. Geographic Variations.

1. Variations within natural populations of "genera" of fresh-water fishes in northeastern Mexico. (*Platypharodon* and *Xiphophorus*). Myron Gordon.

79. In the original plan, circulated by Dobzhansky before his departure, then by Mayr, the Eastern group's meeting was scheduled for 12–13 June. This was cancelled as four of the seven participating paleontologists were unable to attend. See Mayr to Dobzhansky 11 June 1943 in Mayr/Dobzhansky Papers, and Mayr and Stern correspondence in Stern Papers, folder "Mayr, Ernst #1." The schedule change came rather at the last minute, see 1 June 1943 Mayr to Muller in Mayr Papers, folder 82.

80. Spencer's placement in the Committee is discussed in Mayr to Stern 2 April 1943 in Stern Papers, folder "Mayr, Ernst #1."

81. Footnote added at this spot by editor of the *Report of Meetings*, noting, "Professor [Carl O.] Dunbar was suggested as an additional member of the Section of Paleontology."

82. Mayr also invited Carl Hubbs (Museum of Zoology, University of Michigan, Ann Arbor) to attend, but Hubbs declined citing a conflict with his fieldwork schedule (Hubbs to Mayr 18 September 1943 in Mayr Papers, folder 78).

2. Geographic variation among small Triassic reptiles (Procolophonidae) and Pliocene horses (Hipparion). Edwin H. Colbert.
3. Suggestions of geographic variation in the evolutionary record of Hyracotherium in the early Tertiary (Wasatchian) of the Rocky Mountain region. Bryan Patterson.
4. Geographic variation in Atlantic foraminifera. F. B. Phleger. [67]
5. The paleogeographic analysis of the Upper Devonian of Western New York and adjacent region as a basis for the recognition of geographic variation among the pelecypod faunas. K. E. Caster

II. Discontinuity.

1. Time variants versus space variants. The need for standardization of techniques and terminology for joint use of neontologists and paleontologists. Glenn L. Jepsen
2. The (Neontological) species concept in historical perspective. Discontinuity between individuals and populations. Sympatric and geographic speciation. (with examples from ornithology). E. Mayr.
3. Relative growth (Julian Huxley's formula), "mutations" and taxonomy. F. B. Phleger.
4. The genetic basis of discontinuity. Sympatric and geographic speciation. Curt Stern.

III. Rates of Evolution.

1. Differential evolutionary rates among phylogenetic lines and within a single phylogenetic line. (Ceratopsian dinosaurs; fossil carnivores). Edwin H. Colbert.
2. Variations in ratio of gene mutations. External and internal factors affecting rate of mutability, with special emphasis on the latter. M. Demerec.
3. Evolutionary stagnation (Phororhacoid birds); shifts in morphogenetic field (Dentition of Taeniodonta and the fossil armadillo [*sic*] Euphractus); consistent instability (sloths, dicynodonts). Bryan Patterson.
4. Biometric methods applied to the determination of phylogenetic relationships of fossil vertebrates (Permian reptiles; Tertiary mammals, esp. horses). A. S. Romer.
5. Comparative mutation rates in *Drosophila* species. W. P. Spencer.

IV. Evolutionary trends.

1. (Omitted because of lack of time). Parallelism in evolution. A. S. Romer.

2. Evolutionary trends as seen by the geneticist (Random, i.e. not adaptive mutation and selection; “orthoselection”; hidden adaptive values of characters, etc.). H. J. Muller.⁸³

A copy of abstracts of all but two of these papers accompanies this report. [7|8]

B. Specific suggestions made in the course of discussions.

1. Concerning apparently identical arctic and antarctic species of foraminifera: their specific identity should be tested by crossing in the laboratory.
2. Concerning terminology: Subspecies due to divergence in space should be distinguished in terminology from those due to divergence in time. Terms suggested (by K. W. Cooper): “Para-subspecies” and “ortho-subspecies”.
3. Concerning sympatric speciation: Laboratory and field evidence in favor of such an origin of speciation should be assembled in special paper. (Suggested author: Curt Stern).
4. Concerning world-wide parallelism in time-sequence of morphologic types in case of Fusulinids (marine benthonic foraminifera of late Paleozoic): the essential facts should be set forth in special paper. (Suggested author: Carl O. Dunbar).
5. Concerning tropical forest as promising environment for ancestral and moldable types: students of sedimentation should be asked to supply criteria for the recognition of the tropical forest environment in the fossil record and list formations known to be or suspected of being of such origin.

C. Actions taken in business section. / (held on second afternoon).

1. Walter H. Bucher was made acting chairman of the committee to serve for the duration of the war in place of G. G. Simpson. He accepted with the explicit understanding that he is to function mainly as a link between the committee as a whole and the Washington office and that the scientific and organizational activity will be carried on, as before, by the sectional chairmen.
2. It was agreed that the committee should work during this year toward the following ends:
 - (a) foster joint discussions of common problems among geneticists and paleontologists through personal contacts and correspondence.⁸⁴

83. Muller provided an abstract to his presentation, *see* Muller to Mayr 27 September 1943 in Mayr Papers, folder 82. This also is discussed in Mayr to Muller 1 June 1943 in same folder.

84. Mayr took charge of the correspondence project as early as August 1943. Stern did not produce the promised work. A gap in their correspondence lasted from 24 September 1943 to 7 March 1944.

- (b) to plan a symposium, to be published eventually in book form, which will set forth for workers in the two fields the precise nature of the best data now available in the two fields of Genetics and Paleontology that bear on the major problems of evolution. Each section is to select specific topics that represent the most instructive and complete cases and lead to the theoretically most significant conclusions.

Each subject is to be documented by illustrations and tables as full as possible and presented in such a manner that it may be fully comprehended and critically evaluated by the workers in the other field who are not familiar with the details [8|9] of terminology and technique used. In each case the theoretical implications of the results are to be set forth explicitly for those not sufficiently acquainted with the lines of reasoning peculiar to the two fields of science.

It was recognized that such a work involves special difficulties, but that if prepared with adequate care it will prove valuable in stimulating thought and further research in both fields.

Two preliminary steps were outlined, to be carried to completion well before the end of 1943 viz.:

- (a) the selection of topics for the symposium (through the efforts of all members).
- (b) the selection of a relatively small number of references suitable as basic reading for the workers who wish to brush up on modern developments in the other field. Some of the references, accordingly, will be to chapters in larger texts or handbooks. The following members have undertaken to prepare these lists:

Genetics: K. W. Cooper, Curt Stern.

Paleontology: A.S. Romer.⁸⁵

3. The section chairmen and the committee chairmen were to act as an executive committee which is to plan future meetings. The question was left undecided if the final symposium shall be held a year from this date or if more time should be given to its preparation. It was also suggested that a meeting be called for the purpose of formulating definitely the plans for the symposium.⁸⁶

85. None of these volunteers produced a reading list. Instead, Dobzhansky produced a genetics reading list; Simpson, paleontology; Mayr, systematics. These were circulated with *Bulletin* 5; they are included here as Appendices 3–5. Subsequently, Elias produced a bibliography for paleobotany, which was circulated with *Bulletin* 6; it also is included here as an Appendix 7.

86. Part of the Eastern Group met again on 6 December 1943 and decided to initiate letter exchanges to discuss items they saw of eventual relevance for this symposium, recognizing, in Bucher's words, "a consider amount of spade work needs to be done." These exchanges ultimately became the *Bulletins* (Rubey to Harrison 17 December 1943 in NAS Archives, folder "Geology and Geography 1943, Committee on Common Problems of Genetics and Paleontology").

4. It was agreed that this committee shall make it its policy to encourage students in Genetics and Paleontology who have taken their Ph. D. degrees or are about to complete it, to apply for National Research Council Fellowships for the purpose of spending a year studying in the corollary field, the paleontologist studying genetics and vice versa.⁸⁷
5. It was agreed to send letters concerning this meeting to Doctors Simpson and Dobzhansky.
6. Thanks were expressed unanimously to the American Museum of Natural History for the hospitality extended to this meeting.

Glenn L. Jepsen

E. Mayr

Walter H. Bucher [9|10]

Part III / Abstracts / Meeting of Eastern Group, Committee on Common Problems of Genetics and Paleontology / July 24–25, 1943

I. Geographic Variation

Edwin H. Colbert

The study of geographic variation in vertebrate paleontology is of necessity quite different from what it is in modern taxonomy. Students of modern forms may follow relatively minute variations, especially as they are expressed within subspecies in contiguous geographic areas. The student of fossil vertebrates, since he is working only with the internal hard parts and since he must always keep in mind the time element, bases his observations upon larger differences covering greater geographic areas. Thus, his studies are most fruitfully developed along the lines of specific and even generic differences over vast stretches of the earth's surface.

Geographic variation in vertebrate paleontology is best illustrated by the adaptations of certain genera or phylogenetic lines in different regions—the results of migrations or dispersals from central points of common origin. Examples of this may be found, for instance, among the small Triassic reptiles known as procolophonids, and among mammals in the Pliocene horses of the genus *Hipparion*.

Bryan Patterson

Deposits of early Eocene Wasatchian age occur on the western slope of the Rocky Mountains in a number of basins that extend for over 600 miles in an approximate N–S line. Four successive faunal stages in the

87. This plan was discussed further in the Committee's report on 29 April 1944 to the NRC. These efforts were to "induce adequately prepared men in genetics and paleontology" to apply for NRC fellowships. "It is hoped," the Committee suggested, "that such cross-fertilizing studies may yet be initiated through the efforts of the members of the Committee." Two possible candidates were claimed, but not named. Probably, one was Dean Amadon, who was training at the time in the American Museum. Another likely applicant, Bryan Patterson, was drafted.

Wasatchian have been discerned. The evolution of the four-toed horse, *Hyracotherium*, will be discussed, and the horizontal and vertical distribution of characters considered.

F. B. Phleger

Geographic Variation in Atlantic Foraminifera. Range of modern Foraminifera faunas in the Atlantic Ocean has two major aspects. There is a distribution according to depth (in benthonic faunas) and a distribution according to latitude and water mass occurrences, in both benthonic and pelagic species. Both kinds of distribution appear to be related to water temperature and/or other unknown factors. Cold water, high latitude faunas generally contain a smaller population and fewer specimens. All these suggest a genetic control affected by ecologic factors. [10|11]

Arctic and Antarctic faunas are very similar and can be distinguished only by rare diagnostic species. These faunas are not now connected and appear not to have been connected during the Pleistocene ice advance. During the Pleistocene ice advance, Arctic faunas migrated into warm temperate regions.

II. Discontinuity

Glenn L. Jespen

Two aspects of discontinuity, geographic and temporal, meet in systematic practices and their union presents intricate and confused taxonomic situations and concepts.

In studies of contemporaneous forms genetic and spacial [*sic*] discontinuities may be absolute, and the fact that our taxonomic system was devised and calibrated upon the presumption that organic categories are essentially immutable is relatively insignificant. Living groups can be conveniently delimited upon various aspects of the discontinuous or the statistical distribution of their genetic, morphologic, biologic, ecologic, ethologic and other attributes.

However, if evolution proceeds by microgenetic changes there are no genetic discontinuities or morphologic gaps in a complete phylogenetic series, although in such a continuum there may be various sorts of fluctuations, reverses, and rate changes which can be used as bases for taxonomic decisions.

Morphology is the primary basis for taxonomic concepts about fossil groups, and the biologic, genetic and other direct tests for group integrity are inapplicable. Neontologists, in developing non-morphologic and experimental criteria for the lower categorical ranks are automatically excluding fossils from similar treatment.

Standardizations of techniques and jargons would aid investigations of common problems in the interfield between genetics and paleontology, particularly in subjects like discontinuity.

As an example of differences in the practice of systematics may be cited the fact that to many zoologists an indispensable characteristic of subspecies is their capacity for crossbreeding with other subspecies, whereas paleontologists have sometimes delimited subspecies vertically—a temporal guarantee against crossbreeding.

*E. Mayr*⁸⁸

Discontinuity between individuals versus discontinuity between populations.—Is Evolution possible without the origin of discontinuities?—Discontinuities between sympatric species are usually bridgeless gaps. Isolating mechanisms prevent the eradication of such gaps. [11|12]

The origin of these discontinuities can not be understood without a clarification of the species concept. The evolution of the species concept from Darwin to the present. Geographical variation and the polytypic species. The role of geographical isolation for the development of biological isolating mechanisms. The question of sympatric origin of isolating mechanisms among animals (= non-geographic speciation). The widening of certain interspecific gaps (= the development of the higher categories).

F. B. Phleger

Relative Growth, "Mutations" and Taxonomy. The relative growth formula of Huxley (and others) has been applied to analysis of fossil mammals. This formula, $y = bx^a$, (y = size of one part, x = size of another part, b and a are constants), has been extensively used in modern materials. In specimens of different sizes within the same species, the value of a is constant. This suggests that the relative growth relationship has a genetic basis.

Robb has applied this analysis to the skulls of the fossil horse series. His results suggest that evolution in this series was mainly due to mutations for increase in size. Hersh's analysis of titanotheres skulls suggests a similar conclusion. Analysis of the Merycoidontidae indicates that different genera arose both by mutations for increase in size and, also, by mutations of the relative growth relationship. The skull proportions of the different species of Merycoidodon appear to be mainly due to mutations for differences in size.

Curt Stern

On the Genetic Basis of Discontinuity. Examples of open and concealed (heterozygous) polymorphism within a population and within a species. On the number of gene differences between related individuals, populations and species.

88. Mayr re-wrote his presentation on discontinuity, creating an "uncorrected" manuscript that he circulated to some Committee members. "... for the benefit of the paleontologists." Paper and related correspondence circa September 1943 in Stern Papers, folder "Mayr, Ernst #1." Thanks to Michael Dietrich, who brought this manuscript to my attention.

The genetic basis for interspecific isolation. The scheme of dominant complimentary factors in genetic isolation. The equivalence for isolation of genic changes and chromosomal alterations except in polyploidy.

The origin of isolation: genetic vs. non-genetic (geographic, ecological, temporal, etc.). The accumulation of diversities during whatever kind of isolation; the consequent establishment or intensification of genetic isolation; the further increase of diversities.

The origin of discontinuities between coexisting and between successive forms.

The hypothesis of systematic mutations. [12|13]

III. Rates of Evolution

Edwin H. Colbert

Rates of evolution have long interested students of paleontology, and while the exemplification of these rates in the fossil record are well known in a general way, there are many details that need to be worked out, which are at the present time attracting the attention of certain authorities.

Certain aspects of the subject as illustrated by fossil vertebrates might be mentioned. There have been differential evolutionary rates within phylogenetic lines, expressed by the coexistence of related conservative and progressive forms. There have been differential evolutionary rates in single phylogenetic lines at different stages of geologic history, resulting in accelerations and retardations of evolutionary development. Finally there have been differential morphologic rates, whereby separate portions of the organism show different rates of development. Examples of these different expressions of evolutionary rates may be found among the ceratopsian dinosaurs and, among mammals, in the placental carnivores.

M. Demerec

(*Variations in rates of gene mutations*)—Gene mutations are one of the most important primary factors producing the variability essential for evolutionary change. Up to the present it has been possible to influence gene mutability by only a very few external factors, such as X-ray, ultra-violet, neutron and related types of radiation; high temperatures; and possibly certain chemicals. However, it is very doubtful that these external factors are sufficiently powerful in nature to influence the mutability rate to such a degree as to be effective in evolutionary processes.—Ample experimental evidence is available indicating that, in addition to external factors, there are internal factors that affect the rate of mutability. A number of genes are known which are in an unstable condition and change from one allele into another with high frequency. Many such

genes are discovered in plants (variegations), and at least three have been found in *Drosophila*. Genes are known which are themselves stable but which influence the rate of mutability of other specific genes, either unstable (*Drosophila*) or stable (maize). Finally, at least one gene is known (in *Drosophila*) which appears to increase the mutability rate of all other genes. Therefore, it seems justifiable to infer that the genetic make-up of an organism and of a species determines the mutability rate of the genes carried by that organism and species, and thus affects one of the important factors of evolution.

Bryan Patterson

Evolutionary stagnation. The phororhacoid birds appear suddenly in the South American fossil record in the mid-Oligocene. They were by that time completely differentiated into the three families Phororhacidae, Psilopteridae and Brontornithidae. An evolutionary trend may be observed in the Phororhacidae which is slight and orthoselective in nature, involving the rim of the [13|14] antorbital vacuity, the depth of the beak and the amount of descent of the palatine plate below the tomium. With these exceptions, skull size and structure remained nearly constant from mid-Oligocene to mid-Pliocene. Such stability, combined with great specialization and long survival, is unusual among higher vertebrates; the reason appears to lie in the ecological position of these birds in the successive South American faunas.

Shifts in a morphogenetic field. Butler has recently advanced the hypothesis that the dentition may be considered as a morphogenetic field with an antero-posterior axis and regional differentiation into regions of incision, caninisation and molarisation. These regions may shift along the field.

The Taeniodonta exhibit a slow, progressive shift toward enlargement of the third incisor and canine and a forward movement of the molarization region, the end result being that the larger teeth are concentrated around the canine with the cheek teeth decreasing in size posteriorly. Development of this pattern was gradual, taking from early Paleocene to late Eocene, and is fairly typical of the general rate of evolution among animals.

An interesting case of reversal of a trend is exhibited by some extinct armadillos of the *Euphractus* group. In the great majority of armadillos of the family Dasypodidae all the teeth are simple, peg-like structures with little differentiation in size. The living *Euphractus* has a dentition of this type, but certain of its extinct relatives have developed large, caniniform teeth. *Euphractus* is noted for its carrion eating habits, and it is probable that the extinct forms may have been specifically adapted to this habit.

Consistent instability. Small groups that are undergoing speciation are a rather familiar phenomenon; difficult from a taxonomic viewpoint,

they are of great interest and significance to the student of evolution. Certain larger groups, e.g. sloths, dicynodonts, are in a somewhat different category. Members of interbreeding populations here exhibit morphological differences that are as great as those ordinarily encountered between species. Were such situations isolated in time, they might be regarded as cases of active speciation, but this is not true of the sloths at least. To judge from the available fossil evidence, variability in the ground sloths throughout their history was as great as that occurring in their surviving relatives the tree sloths. A taxonomic chaos reflects this situation.

A. S. Romer

Given (1) a series of forms known to be in phyletic sequence and of which we have adequate material, and (2) a knowledge of the relative (not necessarily absolute) time interval between them, one might determine the nature of the evolutionary rate at which changes occur in such phyla, with possibilities of interesting results. In addition there are more purely paleontological applications such as the fitting of new or doubtful [14][15] forms into a sequence, the projection of the graphs of species phyla forward and backward to deduce the nature of ancestral or descended types, time of divergence of phyla, etc. In actual practice we can seldom be confident of the true relationships of species, material is seldom adequate enough for significant results, and time intervals are mainly guess work. However, tentative examples are given dealing with Permian reptile and Tertiary mammal material.

W. P. Spencer

*Comparative mutation rates in Drosophila species.*⁸⁹ Even though special mutation stimulating genes (Demerec, Mampell, Neel, Tiniakov) are known to exist in *Drosophila*, observations over a period of years on diverse stocks of different species should provide some indication of their comparative mutation rates, particularly if these differ widely. The author has found 12 sex-linked visibles at 10 loci in *D. melanogaster*. On observing at least 10 times as many individuals of *D. hydei* only 16 visibles at 13 loci (excepting the special case of bobbed) have been found. These data indicate a sex-linked visible mutation rate in *melanogaster* about 7 times that in *hydei*. Observations on numbers of *robusta* and *funnebris* about equal to the *melanogaster*s indicate low mutation rate as in *hydei*. Analysis of diverse wild populations of *melanogaster*, *hydei* and *robusta* has shown that *melanogaster* carries more autosomal visibles in heterozygous form than either of the other two. *Drosophila funnebris* is peculiar in showing a higher percentage of dominants and poorly penetrant mutants than other *Drosophila* species investigated. The sex-linked bobbed locus in *hydei*, and the autosomal

89. The full text of Spencer's paper is printed in *Bulletin* 3.

loci, net in immigrans, and javelin in transversa show a mutation rate all out of proportion to the general mutation rates of the respective species and to the rate in these loci in other species.

IV. Evolutionary Trends

A.S. Romer

Parallelism. Parallelism in evolution plays an increasingly important part in the thinking of paleontologists but tends to be neglected by the student of modern forms. Examples are cited to show the importance of parallelism in vertebrate evolution. Crudely, examples of parallelism may be classed as (1) parallelism of families within an order, (2) of genera within a family, (3) of species within the genus, with increasing degrees of parallelism. Specific parallelism is presumably common but difficult of proof [*sic*: to prove]. The facts of parallel evolution appear to be perfectly consistent with a neodarwinian application of genetic principles.

[end of Report of Meetings]

BULLETIN NO. 1⁹⁰

MAY 15, 1944

■ [Introduction]

It was suggested in a recent communication of the steering committee that it would be desirable for the members of this committee to use correspondence as a medium for the discussion of common problems in the fields of Genetics, Paleontology and Systematics. Such a written exchange of ideas will have to replace a meeting, the organization of which was found impractical this year because of transportation difficulties and other reasons.

The response of the members of the committee to this request permits the issuance of a first mimeographed discussion bulletin. Considerable additional material is in preparation and it is hoped that it will be possible to bring out another bulletin in the near future. It may be appropriate at this time to call attention once more to the procedure of this correspondence. As stated in the circular letter of January 21, 1944, "The members of the Committee on Common Problems of Genetics and Paleontology are invited to start a discussion by correspondence of topics which fall within the field of interest of the Committee. A member A, say a paleontologist, who would like to know an opinion of one of the colleagues, say a geneticist B, regarding some problem, would write him a letter presenting the issue, and send a carbon copy of his letter to Dr. E. Mayr, as central agency. B would reply to A also by a letter, and would also send a copy of his reply to Dr. Mayr. After a sufficient number of such letters and replies have accumulated in the hands of Dr. Mayr, he will have them mimeographed and will then send the resulting mimeographed circular to all members of the Committee. This would presumably stimulate some other members to enter the discussion by sending letters to each other or to the original correspondents, always sending a copy to Dr. Mayr. When sufficient material is again at hand, another mimeographed circular is prepared and sent to the entire Committee. Much valuable material will accumulate which will be useful to paleontologists as well as geneticists."⁹¹ The address to which the carbon copies of this correspondence should be mailed is:

90. This *Bulletin* carried a heading with the new Committee's title, "Committee on Common Problems of Genetics, Paleontology and Systematics". This heading was repeated on the cover page of each *Bulletin*.

91. A copy of this letter is located in Babcock, Bucher, Chaney, Dobzhansky, Jepsen, Mayr to Simpson 21 January 1944 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1."

Dr. E. Mayr
The American Museum of Natural History
Central Park West at 79th Street
New York 24, New York

It is hoped that the following letters will be the beginning of a fruitful discussion. Any member of the committee who has further questions or comments is invited to communicate with the correspondent most concerned.

The Steering Committee
[cover page |1]

February 5, 1944

Dear Professor Chaney:

The problem of the speed of evolutionary changes in different groups of organisms is among those where a geneticist hopes for guidance from paleontologists. At the suggestion of Dr. C. Epling I have been trying to familiarize myself with the work of your school on fossil Tertiary and Pleistocene floras of North America. I am indeed impressed by the magnitude and thoroughness of this work, but being even less than an amateur in these matters I probably can not yet form a clear idea about the full meaning of the facts discovered by you. Since other geneticists may be in the same condition as I am, perhaps some "discussion by correspondence" may be helpful not to myself alone.

The points which interest me primarily in a paleobotanical paper are (a) how different from the living species are the fossil forms, and (b) where the nearest living relatives of the fossil species are to be found. A paleobotanist is also trying to answer the above questions, but his answers are frequently couched in a language fully comprehensible only to a specialist.

I understand that *Sequoia langsdorfii* Heer is "the Tertiary equivalent of the living *S. sempervirens*", and that *Fagus pacifica* Chaney "appears to be closely related to the living beech, *F. grandifolia*". What I would like to know is this: is it at all possible that *S. langsdorfii* and *S. sempervirens* belong to the same species, and that *F. pacifica* and *F. grandifolia* are also two forms of the same species? In other words, is it certain beyond a reasonable doubt that if a botanist would pick leaves from a tree of *F. pacifica* he would immediately know that this tree is not *F. grandifolia*? Or is it possible that this imaginary botanist would regard *F. pacifica* as a mere aberrant specimen of *F. grandifolia*? I picked these [1|2] two pairs of species merely as examples from your papers, but similar questions arise in my mind as soon as I start to read a paleobotanical paper.

I think that I appreciate the difficulties of answering the above questions. A paleontologist may not be able to compare the fossil and living

species organ for organ. Probably some paleobotanists give a new species name if they are not quite sure that the fossil and the living forms are quite identical, while other paleobotanists use the name of the recent species for the fossils unless they are quite sure that the latter are very different from the former. The presumed living equivalent of the fossil species may be a plant growing thousands of miles from the locality where the fossil is found, and it may be just easier to give to the fossil a separate name than to obtain adequate material on the living species for comparison. Nevertheless, a non-specialist reader of paleobotanical literature wants, I think, to know how much change has there been in various plant genera and families during the time intervals since, say, Pleistocene, or Miocene, or Eocene. Permit me, then, to over-state my questions in a form which may, perhaps, make the answering easier.

(1) Are there any Pleistocene fossil plants known from the United States which certainly belong to species other than those now growing in the United States or elsewhere?

(2) If so, what is the minimum estimate of the number (or percentage) of the species which have disappeared since Pleistocene? (by becoming extinct or by changing).

(3) What would the answer to the questions (1) and (2) be if we substitute "Miocene" and "Eocene" for "Pleistocene"? I realize that the floras of early Tertiary in the United States resemble the modern floras of Central and South America more than they do the present United States flora. [2][3] Because of the imperfect knowledge of the tropical floras some living equivalents of fossils may exist but may not be known. I think, however, that even rough estimates given by you would be very valuable.

(4) I take it that very little is known about the fossil floras of the present day tropical countries. But if the data allow it at all, I would like to know whether there is any positive evidence of changes in the floras of the tropical countries since the early Tertiary. In this case I mean by "changes" not only extinction and transformation of species as in questions (1) to (3), but also changes due to migration of the floras from place to place.

Very sincerely yours,
(Th. Dobzhansky)

March 29, 1944

Dear Professor Dobzhansky:

Before answering your questions, it seems desirable to indicate the general problem which a Cenozoic paleobotanist has to face in determining the specific status of his material. This problem has been discussed in numerous publications written by my associates and by me during the past quarter century, and its most recent consideration is in

the introduction to a volume on the Pliocene floras of the western United States, Pub. 553 of the Carnegie Institution of Washington, shortly to be issued. [Chaney 1944]

For practical reasons, involving the time and space involved and the fact that most of them are represented by dissociated structures in their occurrence, fossil plant species must be considered to be distinct from other known plant species, and from similar living species, unless (1) there are available leaves, fruit and stems, preferably in attachment (a rare occurrence), all of which closely resemble, and fall within the range of variation of, another fossil species or a living species of that genus; (2) they are [3|4] of approximately the same age, that is, occurring in rocks of the same period, and preferably of the same epoch; (3) they occur in adjacent areas, or with no considerable geographic gaps over wide areas. Few Tertiary species meet these requirements. In our consideration of Pleistocene plants, we commonly refer them to modern species since they are represented by numerous seeds identical with those of living plants, as well as similar leaves and stems. In addition their range in most cases coincides rather closely with that of living species. The gap in time is slight; in fact, we may believe that we are still living in the Pleistocene epoch if we weigh much of the paleontological and physical evidence.

Turning now to the questions raised in your letter, I shall answer them in such manner as to provoke further questions and discussion if possible:

(1) Regarding Pleistocene plants.- In their treatment to date, largely under the authorship of Herbert L. Mason, only one species, *Pyrus hoffmanni* Chaney & Mason from asphalt-impregnated terrace deposits at Carpinteria, California [Chaney and Mason 1934a and 1934b, p. 61] has been described as new. But there are other plants, of which *Pinus muricata* is an example, which differ to a degree which might serve as a basis for specific, or at least varietal separation. Pleistocene cones of the Bishop pine have more elongate processes on the cone scales than is typical for cones of living trees; these fossil cones resemble extremes in variation found on certain living trees of the Bishop pine. They also resemble in this respect the cones of a fossil species from the Pliocene of California, *P. masoni* Dorf. Available evidence suggests that the ancestral Bishop pines, as represented by *P. masoni* and by the Pleistocene cones referred to *P. muricata*, were characterized by cones with longer processes on their cone scales than are typical for the modern trees; since certain of the latter have cones of this ancient type, the problem of drawing specific distinctions between them and the Pleistocene [4|5] cones is a difficult one.

(2) Regarding the percentage of species known to have become extinct since the Pleistocene (or since that part of the Pleistocene represented by the latest fossil flora).- Of approximately 70 species described

(there are many more undescribed) from rocks of this age in the western United States, only one is known to be extinct.

(3) Regarding Miocene floras (including the Upper Oligocene).- The number of extinct species is so small as to be wholly negligible. Whether this is a reflection of the attitude of paleobotanists, as outlined in my introductory paragraphs, or is a true indication of the extent of speciation during the past thirty to forty million years, I shall leave for your determination. This much should be said, referring to the Miocene species mentioned in your letter.- (a) Although *Sequoia langsdorfii* Heer is "the Tertiary equivalent of the living *S. sempervirens*", the two species are readily separable. The cone of *S. langsdorfii* is attached at the end of an almost bare twig several inches in length, whereas that of *S. sempervirens* is attached at the end of a fully leaved twig. (b) The leaves of *Fagus pacifica* Chaney, as well as the husks of the nuts, resemble those of *F. grandifolia*, but they average much smaller. Another somewhat younger Miocene species, *F. washoensis* LaMotte, has leaves more slender than are typical for *F. grandifolia*. I have seen leaves of this slender type on trees of the living species in the Cumberland Mountains, and believe I have read that Camp has described them as a distinct species; most botanists would not accept this specific separation, I feel sure. (c) The leaves of *Carpinus grandis* Unger show no recognizable difference from those of the living *C. caroliniana*, but seeds of *Carpinus* in association with these fossil leaves are unlike the seeds of this living species. Summarizing the answer to question 3, most Miocene (Middle Tertiary) plants closely resemble living species, and many [5][6] of them may be considered to fall within the range of leaf or fruit variation. The paleobotanist does not assign them to living species because they are seldom if ever typical for all corresponding living organs, because they are in many cases living far from the regions now occupied by living species, and because they are separated in time by tens of millions of years.

(3A) Plants of the Lower Tertiary (including Eocene, Oligocene—Lower and Middle) are even less readily referable to living species than those of the Miocene. Their leaves are seldom associated with fruits and stem structures, and there are greater discrepancies in their age and range as compared with corresponding living species. Certain leaves may well be referable to modern species, but in present practice none of them are so assigned.

(4) There is little evidence of changes in the floras of tropical latitudes during the Cenozoic era. During epochs of mild climate, certain of the hardier elements migrated north into middle latitudes (Wilcox, Chalk Bluffs, Goshen floras). But since all or most of the plants involved in these movements are still represented in the modern vegetation of the tropics, we may suppose either that some individuals of the species involved remain continuously in low latitudes, or that the migrating species in all cases returned to their original home. The extent

of change in the species during the time involved in Tertiary migrations cannot now be fully ascertained. It is possible that many Tertiary species may be actually distinct from those now living. There are comparatively few known Cenozoic floras of the tropics adjacent to North America which can be compared on a contemporary basis with well known Tertiary floras from the United States. Such comparisons as have been made suggest that at any one time during the Cenozoic, the vegetation of low and middle American latitudes was fairly uniform. Similar evidence, even less conclusive, is available from the floras of Asia. My present opinion [6|7*] is that since the Cretaceous period, the forest vegetation of the tropics has been relatively stable as to species. Any final judgment must be based upon more evidence than is now available.

Summary.- It is clear from the preceding discussion that the paleobotanist is greatly handicapped, in establishing specific identity or separation, by fragmentary material, and by discrepancies in time or space. In these respects he has even greater handicaps than modern botanists, whose opinions regarding specific identities vary greatly. It is impossible at the present time, and may always be impossible, for the paleobotanist to find any specific characters as quantitative as chromosome numbers. Without large fossil collections, it is difficult for him to work on a level of accuracy comparable to that of sounder botanical taxonomists. He must continue to dig into the earth, and to use the best practices of contemporary botanists in his study of what he finds.

Sincerely yours,
Ralph W. Chaney

April 14, 1944

Dear Professor Chaney:

I appreciate greatly your letter of March 29th. To me at least, this letter has justified the existence of our Committee. In this letter of less than three pages, you have clarified the point which was a puzzle to me, namely what is meant by a "species" in paleobotany. It is certain that every paleobotanist knows very well the current conventions regarding what should and should not be described as species. It is very probable that this convention is explained in some of your publications. But our reading outside our own speciality is bound to be a bit superficial, and yet it would be a sad day if we would stop outside reading because of this. The possibility to supplement one's familiarity with the scientific literature in related [7|8] fields by explanations of specific points given by outstanding specialists in these fields is indeed a privilege. I take it that our Committee has been organized for the purpose of extending this privilege to paleontologists, systematists, and geneticists.

I understand, then, that fossil plant species are presumed to be distinct from living or from other fossil species unless their specific identity can be proven. This is rather the opposite of the convention prevailing in at least the better known groups of living organisms, where forms are presumed to belong to the same species unless the contrary can be demonstrated. It is reasonable that, for practical considerations, different conventions may be used in different, even though closely related fields. The important thing is that the conventions be well known for what they are.

The thing which impressed me most from my very slight acquaintance with the paleobotanical literature, is the apparent evolutionary conservatism of higher plants. This impression is, of course, greatly strengthened by your letter. Now, permit me to raise some far-fetched questions in this connection; raising such questions may sometimes be useful to clarify our ideas.

(1) Suppose that an intelligent anti-evolutionist (if such a thing can exist) gets hold of paleobotanical literature, and asserts that the information available in this field proves that the evolution of higher plants has ceased at least since the end of the Cretaceous period. What evidence can one oppose to such an assertion? You say that the forest vegetation of the tropics has apparently been rather stable as to species since the Cretaceous. The evidence for evolution, if any, must, then, be looked for in the temperate floras. Now, I understand that some temperate plant associations (such as grasslands) seem to have arisen during the Tertiary. Does this mean, however, that the species characteristic of grasslands [8|9*] evolved during the Tertiary, or is it possible that new plant associations came about merely by drafting among the Cretaceous or early Tertiary species the forms which were pre-adapted to form a grassland? I understand that I may be asking for too much—for evidence that certain modern plants *did not* exist at a given time. I hope, however, that you see clearly what I have in mind—I am interested in what evidence paleobotany has that evolutionary changes were taking place during the Tertiary and Pleistocene.

(2) This is, really, a variant of question 1, approaching the problem in a different way. In your letter you say that “most Miocene plants closely resemble living species, and many of them may be considered to fall within the range of leaf and fruit variation”. I would like to ask: approximately what proportion, if any, of the known Miocene (or Eocene) plants have changed so much that their living derivatives would be classed as unquestionably different “good species” if the Miocene and the modern forms would be found in the same herbarium?

(3) Plant genetics has produced some of the most striking instances of evolutionary changes. These changes involve, for example, sudden origin of unquestionable new species by auto- and especially by allopolypoidy [*sic*]. Evidence, circumstantial to be sure, but about as

conclusive as could be obtained where a historical problem is involved, shows that some new polypoid [*sic*] species arose as recently as Pleistocene (the work of Edgar Anderson, Babcock and Stebbins, Muntzing, and others). Changes due to E. Anderson's "introgressive hybridization" and to the "danse macabre" of the apogams were going on in recent, past, and almost certainly are still going on. However, as especially convincingly shown by Drs. Babcock and Stebbins, these changes are not what at least a zoologist would call normal method of species formation. They are, rather, opportunistic devices or "get rich quick" schemes which, though sometimes eminently successful for a time, eventually lead to evolutionary stagnation. As a zoologist, but as an intensely interested spectator, [9|10] I wonder whether the plant kingdom furnishes many good examples of speciation of the same kind which fascinate so much the zoological colleagues. By this I mean good polytypic species in which the extreme subspecies differ morphologically about as much as do average sympatric species of the same genus or family, thus suggesting that a species is becoming split into new ones, via geographic race formation. To be really "good" these species should also be free of polyploidy and the rest of the aberrant evolutionary patterns mentioned above. Is it possible that the failure of most botanists to adopt the polytypic species concept (see [Mayr 1942]) is due in part to what is the "typical" or "normal" polytypic species situation to a zoologist being not very common among higher plants? (I am familiar, second hand of course, with some botanical situations which at least superficially resemble the polytypic species of zoologists; for example, Epling's *Salvias* and [Marion] Ownbey's *Calochortus*, but how common are such situations among higher plants in general?).

(4) If species formation via the polytypic species situation is not very common in higher plants, could one correlate this with the apparent high evolutionary conservatism which paleobotanic data seem to indicate? If not, what plausible, even if purely speculative, hypothetical explanation of this conservatism could the botanists suggest?

I realize that in asking the above questions I have to some extent played the role of devil's advocate. I do think, however, that these questions are legitimate, and that answers to them may improve the mutual understanding between zoologists and botanists.

I hope that the above questions may provoke a reaction from not only Professor Chaney but from workers on systematics and genetics of living plants as well. I am therefore sending copies of this letter to Professors Epling and Stebbins for their comments.

Sincerely yours,
Th. Dobzhansky [10|11]

April 28, 1944

Dear Dr. Dobzhansky:

Chaney has sent me a copy of his letter to you dated March 29th and states that he has a reply from you which he wants to discuss with me. Meanwhile Stebbins has shown me his copy of your letter to Chaney dated April 14, and suggested that I write to you about the evidence on evolution in *Crepis*. I am glad to do this because this genus provides exactly what you are asking for, namely, evidence from the plant kingdom that: (1) progressive evolution has been going on since early Miocene; (2) that the main features of the process are strictly comparable to those which characterize the evolution of animals; (3) that the "most primitive" and "most advanced" types in the genus are actually *very old* and *comparatively young* species; (4) that numerous polytypic species exist now which appear to be in process of speciation. I will take up these four points in sufficient detail to give you a fair idea of the nature of the evidence.

1. Early Miocene was established as the approximate time of origin of *Crepis* on the basis of distributional, ecological and paleobotanical evidence. In our monograph on the American species Stebbins and I concluded (p. 35) that the two oldest of those species must have originated during Miocene [Babcock and Stebbins 1938]. We also have distributional evidence from other sections of *Crepis* (diploid species) which can only be interpreted on the basis of pre-Pleistocene origin and distribution. Furthermore, the distributional evidence on the genus as a whole leads inevitably to the conclusion that the center of origin for the genus is northern Central Asia (the Altai-Tien-Shan region). This conclusion has been verified by many colleagues, among whom the following names occur to me at this moment: [Ralph Works] Chaney, [Herbert Louis] Mason, [G. Ledyard] Stebbins [Jr.], [Maxim K.] Elias, [Carl] Epling, [Harry Dunlap] MacGinitie, [Carl William] Sharsmith, Sauer⁹² and Alden Miller. Finally the fossil evidence consists of seeds of three species which were found in middle Pliocene clay beds on the Dutch-German border. The original identification was made by European [11|12] botanists and, from the excellent lithographs in the published report, I am satisfied that they are comparable to three of our present-day more primitive species. The location of the deposits was in the huge Pliocene delta of the Rhine and it is safe to assume that the seeds were transported from the central European uplands. This area is about 6000 kilometers (3700 miles) from north Central Asia. In order to have migrated such a distance before mid-Pliocene, these species must have originated during the Miocene. The sum total of the evidence calls for early Miocene.

92. The identity of "Sauer" is not clear.

2. That the main features of evolution in *Crepis* are comparable to those found in many animals is clear from the following facts. The American species (and a comparable small group of polyploids in Asia, section 18) are merely side issues from the main line of development in the genus. This line of development involved the progressive decrease in chromosome number, step by step, from $n = 6$ to 5 to 4 to 3 (cf. [Babcock 1942: 146–147]). The great majority of the species in the genus belong in this series. The evidence on karyotype evolution is directly correlated with the evidence from morphology, physiology, genetics, cytogenetics and distribution to necessitate the conclusion that, along with the progressive reduction in chromosome number there has been progressive modification of the plant and its parts, through reduction in size and the development of various specialized features. Finally, the convincing demonstration by Hassan Tobgy (see reprint recently sent you from [Tobgy 1943]) that the 3-paired species, *C. fuliginosa*, must have originated from a 4-paired ancestor, and some comparable evidence of Mrs. Walters (unpublished) that a certain 4-paired species must have originated from a 5-paired ancestor, are of basic importance. They verify our earlier assumption that the progressive reduction in chromosome number was the result of unequal reciprocal translocations between non-homologous chromosomes. Furthermore, a much wider inference seems now to be justified, namely, that arithmetic series of chromosome [12|13] numbers in both animals and plants have been produced by progressive decrease (or increase) in number resulting from reciprocal translocations primarily.

3. That the most primitive *Crepis* species are very old (early Miocene) and the most advanced, comparatively young (Pleistocene), follows inevitably from the evidence on center of origin for the genus, the time required for the present world-wide distribution, and the fact that all of the most advanced, i.e., youngest species are concentrated in the Mediterranean region (sen. lat.). That these youngest species or their immediate ancestors must have been subjected to increasing dessication [*sic*] of the climate during Pliocene is generally understood. Furthermore, the most advanced, and presumably the youngest, of all these species are highly specialized desert annuals which exist today along the northern edge of the Sahara. It is safe to assume, therefore, that they have developed since the Pluvial part of the Pleistocene epoch.

Another illustration involves the three very close diploid species, *C. neglecta*, *C. fuliginosa*, and *C. cretica*. The earlier steps in chromosomal transformation, which resulted eventually in the 3-paired *C. fuliginosa*, probably occurred not later than early Pleistocene when Crete was still connected with the Balkan Peninsula. These initial chromosome changes may have occurred in plants distributed in the now submerged region between Greece and Crete and been followed by southward migration of the new form destined to develop into the 4-

paired *C. cretica*. The later submergence of this region left *C. cretica* completely isolated under increasingly arid insular conditions, so that, through gene mutations, it has become an even more reduced species than *C. fuliginosa*. Subsequent chromosomal transformations, occurring in plants restricted to southern Greece, produced the 3-paired form destined to develop, through accumulation of gene mutations, into *C. fuliginosa*. The remnant of the parental 4-paired species developed into *C. neglecta* which is now distributed from northwest Asia Minor through the northern Balkan Peninsula [13|14] to Italy. Since all these assumptions are consistent with evidence from present-day distribution, comparative morphology, cytogenetics and paleogeography, we may conclude that in this small group speciation was initiated by chromosomal transformations which led eventually to reduction in chromosome number and that differentiation was augmented by the accumulation of gene mutations under the influence of migration, geographic isolation and natural selection.

4. Polyploid species. Ignoring the polytypic species of the American and Asiatic polyploid complexes (sections 15 and 18), there are 15 polytypic species of *Crepis*, i.e., species in which subspecies are recognized. Of these, 12 have been examined cytologically and they are diploid species. Of these 12, three are fairly primitive species and the other nine are more advanced species. Of these advanced, polytypic species the situation in *Crepis foetida* (cf. [Babcock and Cave 1938]) is typical. The subspecies are partly isolated geographically, but they overlap and intergrading variants occur. The stage is set for the development of species either through spatial isolation or the creation of some sort of genetic isolation. In addition to these diploid species in which subspecies have actually been recognized, there are several others in which further research may result in the recognition of subspecies. Then there are still others in which, even though subspecies may not be recognized as yet, still morphological and presumably physiological gradients do exist. Such a species is the 3-paired *C. capillaris* of western Europe. A form in southern Spain has actually been described as a species (*C. gaditana* Boiss.) but this is reduced to a minor variant in my monograph.

Sincerely yours,
E.B. Babcock [14|15]

May 1, 1944

Dear Dr. Dobzhansky:

Your letter of April 14 to Dr. Chaney raised a number of questions of fundamental importance to students of evolution; paleontologists, geneticists, as well as plant geographers. I shall try to answer them from

the point of view of the plant geneticist and the student of present day distribution in plants. You will see that my answers, based on a more or less cursory survey of a number of groups of flowering plants, agree completely with those given by Professor Babcock on the basis of his intensive study of the genus *Crepis*.⁹³

In regard to question 1, I do not feel so sure as Dr. Chaney apparently does that “the evolution of higher plants has ceased at least since the end of the Cretaceous period”, and that “the forest vegetation of the tropics has apparently been rather stable as to species since the Cretaceous”. I agree that most families of Angiosperms, and probably all of those containing predominantly woody species, were well differentiated by the end of that period. Nevertheless, a large number of genera, particularly the herbaceous types, have present-day distribution much more in accord with the hypothesis that they were differentiated during the Tertiary period, and nearly all annual species seem to be late Tertiary or Pleistocene in origin. Some herbaceous families, like the Valerianaceae and Dipsacaceae, have monocentric distributions, with their species largely confined to regions geologically and floristically recent, and therefore probably are not earlier than mid-Tertiary in origin. In regard to the forest vegetation of the tropics, Chaney and his fellow paleobotanists have shown clearly that many modern species either existed in their present form or had closely related relatives in the forests of the early Tertiary and Cretaceous periods, but the very nature of the fossil record precludes any statement as to whether modern species not in the record did not exist. I should like Dr. Chaney to [15][16] answer this letter, giving his opinion as to whether the absence or scarcity in the Tertiary and Cretaceous fossil record of such woody tropical families as the Melastomaceae, Flacourtiaceae, Guttiferae, Sapotaceae, and Rubiaceae, all of them very rich in modern genera and species, is due to the fact that members of these families are not suitable for preservation, cannot be recognized when found, or were actually absent or poor in genera and species during the earlier geological periods. The tropics at present are famous for the diversity of their vegetation and the large number of species present in any forest area. Could not this be due partly to the gradual accumulation of species and genera evolving through the ages, and to the existence of new species side by side with old ones? In the herbaceous flora of the tropics, particularly the epiphytic flora, the genera are very largely restricted to a single continental area, in contrast to many woody genera which tend to be pan-tropical. Furthermore, these epiphytes, as in the orchids and Bromeliads, are highly specialized types, which both from the distributional and mor-

93. Babcock, Stebbins, and Jenkins (1942) and Babcock (1944) draw basic conclusions about *Crepis* later elaborated in detail by Babcock's (1947) major monograph. This was submitted for publication in the summer of 1943 but publication was delayed by the war.

phological standpoint seem to be recent in origin. In the tropical orchids, intergeneric hybrids can be made with great ease, indicating that the genera are poorly differentiated genetically and probably relatively recent in origin. I believe, therefore, that a good case can be made for the hypothesis that certain elements of the tropical flora are relatively recent in origin and still in an active state of evolution. Unfortunately, the classification of tropical plants, except in certain particularly well-known areas, is still hardly more than in the exploratory stage, so that we know little about whether or not polytypic species exist in modern tropical forests.

In regard to the species of temperate associations, such as grassland, that have arisen during the Tertiary, the evidence given by Dr. Elias, in his "Tertiary prairie grasses and other herbs from the high plains" indicates that not only do these associations contain species not found in the earlier associations, but that the modern species found there are themselves [16|17*] very different from their middle or late Tertiary ancestors [see also Chaney and Elias 1936; Elias 1942]. This is borne out by the modern distribution of species in such grassland genera as *Stipa*, *Andropogon*, and *Bouteloua*, as well as in the herbaceous species of savannah and desert areas. In them the *genera* seem to be largely mid-Tertiary in origin, but the *species* have distributions restricted to recent areas, and tend to have their nearest relatives in the same or adjacent regions, so that their more recent origin is strongly suggested, in support of Elias' fossil evidence.

The second question is not for me, but in regard to question (3), I believe that one can safely say that even when polyploids and apomicts are disregarded, the number of species of Angiosperms which has evolved since the middle of the Tertiary period is as large as that of all land vertebrates put together. Babcock has given a clear account of the situation in *Crepis*; in many other genera of the Cichorieae, such as *Lactuca*, *Launaea*, *Scorzonera*, *Malacothrix*, *Microseris*, and *Stephanomeria* the situation is essentially the same. The extensive, largely unpublished work of Clausen, Keck and Hiesey on the tribe Madinae describes a similar situation in this endemic Californian group of Compositae.⁹⁴ I have good examples of polytypic species in *Lactuca* and *Malacothrix*, while the Madinae are full of them. Good examples of polytypic species of a woody, strictly diploid genus inhabiting geologically and climatically recent areas are to be found in the volume of McMinn, Mason and others on the genus *Ceanothus*, as well as in unpublished work by McMinn on the same genus [Van Rensselaer and McMinn 1942]. Certain complexes of the subgenus *Cerastes* in

94. As a team, Jens Clausen, David Keck, and William Hiesey produced a large number of papers during their collaborations in the 1930s and 1940s. Clausen, Keck, and Hiesey (1939; 1940) summarize this research. French (1989) provides the relevant bibliography; Hagen (1981) and Smocovitis (1988; 1997) give some historical context to this research.

particular seem to contain species recently evolved or in the making. On the other hand some species of this genus, like *C. arboreus* and the Mexican *C. coeruleus*, are undoubtedly ancient. It is true that polytypic species are not the usual type in the higher plants as they are in vertebrates, but I believe that they are nearly or quite as common as in some groups of insects. In a paper in the American Journal of Botany for 1938 I pointed out that polyploids are less [17|18] common in annuals than in perennial herbs [Stebbins 1938]. Most botanists agree that the modern annuals are relatively recent in origin, so that the evolution of these specialized types in the past two or three million years on the diploid level seems well established. In some genera, like the annual species of *Bromus*, *Festuca* and *Hordeum* and the genus *Aegilops*, a pattern of polyploidy has been superimposed on the original diploid one, but this must be very recent, with the diploid ancestors not older than the Pliocene epoch.

In answer to question (4), it must be pointed out that the genera which enter into the paleobotanic data contain a large number of polytypic species among their modern representatives. The pines, firs, oaks, poplars, walnuts, elms, alders, hazels, madrones, and other groups strongly represented in the fossil record have few or no polyploid series in their modern species. Although certain particularly conservative ones, like *Sequoia sempervirens* seem to be relic members of ancient polyploid complexes; others, like *Sequoiadendron giganteum*, definitely are not. *Pinus ponderosa* and *P. contorta*, *Populus tremuloides*, *Quercus dumosa*, *Alnus viridis* and *A. incana*, *Corylus rostrata*, and *Acer negundo* all would in my opinion turn out to be good examples of polytypic species when studied with this concept in mind. My speculation as to the apparent conservatism of the plants represented in the fossil record is as follows.

I believe that rates of evolution have been very different at different times and in different organisms. The slow, steady evolution considered to be the normal thing by many evolutionists has very likely held true for the marine organisms which form the bulk of the fossil record in animals, because the marine environment is relatively little differentiated into local regions, and rarely undergoes geologically sudden changes. On the other hand, in terrestrial organisms, both animals and plants, the alternation between geologically stable and rapidly changing environments, as well as the existence of radically different environments in adjacent parts of the same [18|19] land area, has caused alternations between periods of explosive evolutionary activity and periods of relatively slow evolution or even stagnation. If a particular environment is expanding, any group of organisms containing structural features preadapting them to that environment, as well as a high degree of heterozygosity, will undergo rapid evolution. If, on the other hand, a type of environment is contracting, organisms adapted only to that environment will diminish in numbers, evolve slowly, or fail to evolve at all.

Thus, in the early and middle part of the Cretaceous period, the Jurassic mountain masses were being peneplaned, and the equable mesophytic type of environment suitable for forests was expanding. The early Angiosperms possessed structural features of the flower and seed which made them better adapted for spreading into these new forest areas than their Gymnospermous predecessors of the Jurassic period. Not the least of these preadaptations were the various structures which promoted insect pollination, since the families and orders of insects may very well have been evolving rapidly at that time. In fact it is possible to conceive of most of the differences between the major families of Angiosperms as different ways of solving the two problems of cross pollination by means of insects, and seed dissemination by means of wind, animals, and other agencies. The rapid evolution of families and genera of woody Angiosperms would therefore be expected during the early part of the Cretaceous period. Between the middle part of the Cretaceous and the end of the Eocene epoch of the Tertiary period, large areas having a mesophytic, equable climate continued to exist, so that the evolution of species and genera of woody Angiosperms continued, though at an increasingly slower rate. Throughout the middle and latter part of the Tertiary period, and continuing to the present, the areas of the earth having a climate suitable for forests have been gradually decreasing. Hence the larger woody species and genera have been decreasing in their geographic area, while many have become very rare or extinct. In such groups the recent climates have [19|20] exercised too rigid selection to promote rapid evolution, while the insect fauna of these areas has likewise been relatively conservative in its evolution, perhaps for the same reasons.

On the other hand, the expansion of grassland, savannah, desert, and mountain areas from the middle of the Tertiary to the present has promoted rapid evolution in such families as the Gramineae, Cyperaceae, Compositae, and Boraginaceae, which possess structural adaptations in both their vegetative and reproductive parts adapting them particularly well to such areas.

In animals, particularly terrestrial vertebrates, the situation is altered by the fact that competition between animal species is relatively keen, and to an animal an alteration in the biotic environment is far more significant than it is to a tree. Predation is practically unknown in plants, and an adult tree rarely if ever dies of starvation through being robbed of its sustenance by its competitors. The ponderous, inefficient big tree or cycad can live for thousands of years beside the more efficient oak, fir, or palm, but primitive, inefficient carnivores or herbivores are quickly eliminated by their more efficient relatives. Hence a static or decreasing secular environment produces evolutionary stagnation relatively quickly in plants, but in animals evolution does not slow down until both the secular and the biotic environments have become stable.

These speculations have covered a rather wide field and I hope will be taken up and criticized both by yourself and others whose experience is greater than mine.

Yours very sincerely,
G. Ledyard Stebbins, Jr.

March 7, 1944

Dear Dr. Colbert:

The geneticist can observe the rate of mutation at a given gene locus and by studying a number of gene loci, he can make an estimate of the [20|21] total mutability of a given species. However, one gains little from knowing this figure, if one is interested in the rate of evolution. It is now being realized that the speed of evolution depends on many additional factors, of which the degree of selection (selective pressure) and the size of the effective breeding population are perhaps the most important. It is for this reason that the geneticist must turn to the paleontologist for advice.

Paleontologists, and particularly the students of fossil mammals, have studied numerous phylogenetic lines of which the fossil record is fairly complete. They can determine which of the lines change fast, and which slow. They can observe when a sudden change in this rate of evolution occurs. It would be interesting to the student of evolution, who is not a paleontologist, to have some concrete information on these points. I believe, you have gathered some evidence in regard to certain families of carnivores.

But beyond the mere statement of facts, it would be interesting to establish casual relationships. Is it true that periods of environmental change (climatic upheavals) coincide with periods of rapid evolutionary change? To give an affirmative answer one would have to prove that an acceleration of evolutionary change occurs contemporaneously in all or at least in the majority of the lines. What is the evidence on this point?

Another question that interests me vitally is the correlation between population density and evolutionary change. One would expect on the basis of Sewall Wright's formulae—other factors being equal—that rare species evolve more rapidly than abundant ones, also that sedentary species evolve more rapidly than migratory ones. Is there anything in the fossil record either to substantiate these conclusions or to contradict them? Is there any evidence that "rare fossils" belong to particularly rapidly evolving lines?

I believe it would facilitate a better understanding of the [21|22] process of evolution, if you could present some evidence concerning the above asked questions.

Very sincerely yours,
E. Mayr

March 20, 1944

Dear Dr. Mayr:

Your letter of March 7 asks for certain information, that may or may not be supplied by the study of fossils, regarding the rate of evolution. There are essentially three questions for which answers have been requested.

1. What is the evidence as to changes in the rate of evolution?
2. What is the evidence as to relationships between such changes, if they exist, and environmental changes as revealed by the geologic record?
3. What is the evidence as to population density as it affects the rate of evolution?

These questions will be taken up separately and in order.

1. Changes in the rate of evolution.

To anyone who has made a careful study of fossils there can be no doubt but that there have been changes in the rate of evolution, for these changes are in the record. There is no escaping their reality. Some lines evolve slowly, others rapidly. Any particular line may evolve at different rates during different geologic ages—there are accelerations and retardations in the rate of evolution.

For instance, in the development of the two orders of dinosaurs during Mesozoic times one is struck by the steady and comparatively slow development of the gigantic saurischian sauropods throughout the extent of the Mesozoic with the relatively rapid evolution of the ornithischian ceratopsians—the horned dinosaurs—in Upper Cretaceous times.

A parallel case is to be seen in mammalian evolution in the [22][23] development of the fissipede carnivores. Compare, for example, the steady and progressive evolution of the canids, from Lower Oligocene to Pleistocene times with the almost instantaneous development of the felids at the beginning of the Oligocene. This latter group is particularly interesting; it appeared suddenly, almost full-fledged, and since the Oligocene, when the cats attained essentially their modern status there has been relatively little progression in evolution. Here is a fine example of a change in the rate of evolution.

An opposite extreme is to be seen in certain modern viverrids, which have retained essentially the structure of Upper Eocene ancestral fissipedes.

Thus it may be seen that there are not only differential rates of evolution in different phylogenetic lines, but also differential rates in a single line of evolution.

The subject may be followed along still other avenues of approach. We have been considering animals *in toto*, in the preceding discussion of

differential evolutionary rates. But the same considerations apply to definite, limited portions of the body in any particular line of evolving animals. That is, some portions of the body may evolve at a different rate than other portions of the body.

A good example of this is to be seen in the modern aard-varks. These are commonly regarded as highly specialized mammals, which is true so far as the skull and dentition and to a lesser extent, the feet are concerned. But except for the toes, the postcranial skeleton in the aard-vark is essentially that of a Paleocene mammal, such as the genus *Ectoconus*. The aard-vark has become specialized in its skull and teeth because of its highly specialized diet, and in its feet because of its burrowing habits. But otherwise, in the structure of the vertebral column, the ribs, the pectoral and pelvic girdles, the arms and the legs, the aard-vark shows but little [23|24] progression beyond the stage attained by the Paleocene mammal, *Ectoconus*, some 50 million years ago.

All of which goes to show that the rate of evolution is a big subject, with many ramifications, of which but a few have been suggested here.

2. Environmental changes and changes in the rate of evolution.

This is a much more difficult problem than the one last discussed, for the evidence seemingly is contradictory. Thus, from what has already been said, it is apparent that the rate of evolution in closely related phylogenetic lines may at the same time be slow and fast, without any particular relationship to the environmental conditions. We know that the viverrids, which were evolving slowly, and the canids, which were evolving more rapidly but at a steady rate, must have lived under the same environmental conditions as did the felids, which went through a major portion of their structural advancement almost instantaneously, from a geological point of view. This is an example where climate or environment seems to be of little or no consequence. Moreover, there seems to be no accounting on the basis of geological evidence for the sudden flowering of the felids on the grounds of a sudden change in environment.

On the other hand, it would appear that there have been certain critical times in earth history when evolutionary development has been greatly accelerated. Such are the transitions between great geological epochs, as for instance the change from Paleozoic to Mesozoic and from Mesozoic to Cenozoic.

The inauguration of the Mesozoic epoch, in Triassic times, appears to have been marked by the rise of new and advanced forms of vertebrate life. It was then that the extensive radiation of the archosaurian reptiles took place from a thecodont base. It was then that the mammal-like reptiles rapidly attained the culmination of their development, during which certain [24|25] branches were transformed into the mammals.

Similarly, the transition from the Mesozoic to the Cenozoic epochs was a time marked by great evolutionary development, for this was the

period during which the placentals became widely established along varied lines of adaptive radiation.

3. Population density and the rate of evolution.

The difficulty in formulating an answer to this question is that of getting a balanced picture of past populations from the fossil evidence. So many qualifying factors are involved in the process of fossilization that it is almost impossible to obtain anything like the true picture as to animal populations long since extinct. This does not mean that we lack fossil evidence; indeed our fossil evidence is in many cases remarkably complete, so much so that we can follow the evolution of a particular phylogenetic line step by step. It does mean that our evidence is very apt to be unbalanced.

For instance, horses and camels are very abundant in the Tertiary continental fossil bearing sediments of western North America, and it is evident that these animals roamed the former plains of the west in great herds. Insectivores are relatively rare and rodents, while common, are not abundant to the degree that horses and camels are abundant. Which simply means that conditions were favorable for the preservation of the horses and camels while they were not so much so for the smaller animals, in which the bones were more fragile. The ecologic balance of a past era is not preserved in its fossil record.

With these considerations in mind, and making the proper allowances for modifying factors, we can still arrive at certain conclusions as to the rate of evolution and population densities. Thus by the abundance or scarcity of fossil material and by an analogy with present day animals, there is good [25|26] reason to think that the ichthyosaurs were rather abundant in the shallow seas of Mesozoic times. Moreover, like the modern porpoises, the ichthyosaurs must have been widely ranging animals, swimming across great distances of fairly open waters. Probably they were gregarious. Yet these were highly specialized reptiles, showing a fairly rapid rate of evolutionary development—just the opposite of what might be expected according to the Sewall Wright formula.

Another example might be cited. The true elephants appeared in late Pliocene times and went through the course of their phylogenetic development in the comparatively short stretch of one million years that constituted the Pleistocene period. This involved a considerable amount of evolutionary development, especially in the skull and dentition. Yet these animals, as shown by their fossil remains, were abundant and widely spread. They ranged across great continental areas in what must have been large herds. Here again we see a rapid rate of evolution coupled with a high population density—at least for a large mammal—in animals that moved about as freely and to as great distances as almost any forms in the history of vertebrate evolution.

The Rhynchocephalia is a group of reptiles represented at the present time by the single genus, *Sphenodon*. This is a very old reptilian line, dating back to the Triassic, and represented by various genera in widely separated portions of the world. If we can believe the fossil evidence, this group was never a very abundant group; it is probably that in the past, as at present, these reptiles were not common in the sense that most of their contemporaries were common. In spite of the evidence for the comparative rarity of the rhynchocephalians over long phases of earth history, we can find little evidence for a rapid rate of evolution in this group. In fact, these reptiles are noteworthy because of their conservatism.

The leptchoerids were artiodactyls that lived in North America in early Tertiary times. They were descended from and not greatly advanced [26|27] over certain primitive dichobunids, which were the ancestral stock for all of the even toed hoofed mammals. The leptchoerids are noteworthy because of their persistence and their rarity. If the fossil record gives anything like a true picture, it shows that these mammals failed to evolve to any great degree, even though it would seem that they were comparatively rare and probably rather restricted in their movements.

Thus the Sewall Wright formulae, that rare species evolve more rapidly than abundant ones and that sedentary species evolve more rapidly than migratory ones, while logical and apparently valid as based upon modern work in genetics, is not necessarily applicable to the field of paleontology. Probably examples can be found in the fossil record to uphold these formulae, but as has been shown above, there is a considerable mass of evidence which may be interpreted as showing effects the opposite of those postulated by Wright.

It is my personal opinion that rates of evolution are inherent in phylogenetic lines. Perhaps this is no explanation. But according to the fossil evidence now at hand it would seem as though some phylogenetic lines have evolved rapidly, others slowly, for no apparent reasons that can be seen in the environment, in the density of populations and the like. Some groups have been stable, others plastic, some have been "progressive", others "conservative". The foundation for these differences certainly must have been in the genes and chromosomes, but I doubt whether outside factors such as environment or population density have necessarily been important in determining the rate of evolution. Could not rates of evolution be dependent in part upon such things as the stability of chromosomes, the ease of difficulty of gene transpositions and the like? It is probable that the answer is one involving many complex, interrelated factors.

Such are the thoughts of one who sees the fossil evidence. And [27|28] in any serious discussion of evolution the fossil evidence must be taken into account, because it is there—it cannot be dodged. Theories based upon the work done in genetics and experimental biology are

valid only if they accord with the evidence of evolution as it is plainly shown to us by the fossil record extending over many millions of years. It is this time element that makes the contribution of paleontology so valuable to the modern synthesis of biological and geological thought. It is important always to keep the sense of time in mind—almost anything can happen provided there is enough time.

Very sincerely yours,
Edwin H. Colbert

[**end of *Bulletin 1***. A two-page mailing list of Committee members was appended to *Bulletin 1*. This is presented here as Appendix 2.]

BULLETIN NO. 2⁹⁵

JUNE 26, 1944

The issuance of Bull. No. 1 resulted in an accelerated exchange of letters and permits the issue of a second bulletin at this early date. Several of the letters definitely clarify controversial problems, others seem to open up new questions. There is every reason to believe that the stimulating discussion between the members of the committee will continue, and that it will be possible to issue a third bulletin early this fall. As heretofore a copy of all this correspondence should be mailed to Dr. Mayr. It would facilitate the copying of the letters, if the clean, original copy were sent to Dr. Mayr and the carbon copy to the respective correspondent.

[signed]
The Steering Committee

The contents of this bulletin are as follows:

1. On the number of genetic differences between individuals, populations, and species. On possible genetic devices of sympatric speciation. Mayr to Stern, p. 1.—Stern to Mayr, p. 2.
2. On the correlation between breaks in phylogenetic series and gaps in fossil evidence. Jepsen to Caster, p. 7—Caster to Jepsen, p. 8.
3. On the concepts and terminology of vertical subspecies and species. Jepsen to Mayr, p. 10—Mayr to Jepsen, p. 11.
4. On the rate of evolution in plants. Epling to Dobzhansky, p. 17.
5. On the existence and relative importance of polytypic species among plants. Epling to Dobzhansky, p. 24.
6. On the correlation between population structure and rate of evolution. Wright to Mayr, p. 31.

[cover page |1]

March 7, 1944

Dear Stern:⁹⁶

I would like to address to you an inquiry concerning the number of gene differences between individuals, populations, and species. I know that

95. This *Bulletin* was rushed to production. The aim was to spend the remainder of funds allocated from the NRC before the end of the fiscal year.

96. The source letter includes an introductory paragraph that Mayr partially omits in this *Bulletin*. The omitted text is "I trust that you have received the letter [21 January 1944] which was sent to all members of the Committee on Common Problems of Genetics and Paleontology. In this letter the suggestion was made that members of the Committee should correspond with each other concerning unsolved or otherwise obscure problems within the scope of the Committee. Following this suggestion...." At this point, the letter printed in the *Bulletin* begins (Mayr to Stern 7 March 1944 in Stern Papers, folder "Mayr, Ernst #1").

you have collected considerable information on this point for last summer's meeting and that you will be able to answer my inquiry without too much additional research. Please permit me also to state the reasons for my inquiry.

In 1900 De Vries came out with his mutation theory. According to this theory new species originate by mutations, that is by sudden and drastic reorganizations of the germ plasma. Later workers, in particular Morgan and his school, showed that the majority of mutations were rather inconspicuous, in fact the most recent evidence seems to indicate that most mutations have effects that are hardly visible. These findings were corroborated by a different line of evidence. It was found on close analysis that different individuals of a single interbreeding population usually differed in numerous genes, no matter how homogenous such a population appeared on casual inspection. The conclusion had to be drawn from these and other observations that mutations occur frequently and that even a multiple mutational difference between individuals was not necessarily associated with a species difference.

This point is of very great importance when it comes to explain the origin of isolating mechanisms between species. The greater the number of gene differences is, which forms the genetic basis of the isolating mechanisms between two closely related species, the less likely it is that these differences could have arisen between two sympatric or contiguous populations (remember: gene flow, heterozygosity).

It is well known that polyploidy provides for a mechanism in plants whereby the origin of a new species can be accomplished by a single step, a single mutation. Polyploidy is rare in animals and can not be [1|2] considered a normal speciation process, at least not in the higher animals. Rather their species differences are nearly always due to an accumulation of small mutational differences. What I would like to know from the geneticist, is: What is actually known concerning the number of genic and chromosomal differences between individuals of the same breeding population, between several natural populations of the same species, and between good species? What are the minimum figures and what would be your nearest estimate? I realize that there are two great difficulties in answering these questions. The first is that very few concrete data are available at the present time, and the second is that the figures will be different for every pair of species. I do not expect an exact figure for the mentioned reasons. However, would you estimate that two closely related species differ on the average by 50, or by 100, or by 500, or by 1000 genes? It would seem to me that it would stimulate the discussion if you would make some estimates, on the basis of our present knowledge (or ignorance).

Sincerely yours,
E. Mayr

May 13, 1944

Dear Mayr,

In a recent letter you asked me some questions concerning the number of gene differences between individuals, populations and species. "What are the minimum figures and what would be your nearest estimate?" ... "...would you estimate that two closely related species differ on the average by 50, or by 100, or by 500, or by 1000 genes?"⁹⁷

You clearly state that you do not expect figures and on this presumption I shall give some answers related to restricted specific cases.

1. Differences between individuals of the same species.

a) In a wild population of *Drosophila melanogaster*, in Russia, Dubinin tested 4140 second and third chromosomes. They contained 410 lethals and 1621 visible [2][3] allelic differences (though not all of these were different from each other).

b) In *Drosophila pseudoobscura* Sturtevant and Dobzhansky studied chromosome III. They found, in different populations, from 12 to 21% chromosomes with lethals. Besides, numerous semilethals and other genes affecting viability properties are known to exist.

c) In wild populations of the snapdragon *Anthirrhinum [sic]*, in Spain, Baur found many populations to be heterozygous for numerous genes containing for instance more than 25 alleles affecting flower color, sufficient to extract, by inbreeding and combination crosses, a very large number of different populations known from other parts of Spain.

d) In the human species we know of many genetic differences in regard to morphological, physiological, and immunological properties. Many of these are dependent on multiple loci. If we think of the innumerable cases of rare recessive homozygotes, the genes for which are rather frequent in heterozygous state, I believe the average difference between 2 humans may well be counted by hundreds of genes—perhaps rather more than less.

e) Add to this that probably many genes exist in numerous iso-alleles i.e. alleles which in many genetic backgrounds give indistinguishable effects but, as shown by specific backgrounds, are really different from each other.

The examples given do not strictly answer your question. They give data as to the number of genetic differences found in many individuals of a group. You are mainly interested in the total number of differences between any *two* individuals. Since, in diploid organisms, each locus in two individuals is represented by four genes, the maximum difference per locus is 2. How many loci may be involved in differences between two individuals is really unknown. Considering the existence of isoalleles

97. Ellipses added either by Mayr (as editor) or Stern (as author).

together with other alleles determining slight differences I believe the number of genetic differences to be quite high (whatever this means). [3|4]

2. Differences between different populations.

While many of the differences quoted above are concealed, heterozygous recessive, the present question relates to those differences which serve to distinguish populations. They will be due to $\pm$ homozygous differences which are superimposed on the individual differences—and similarities!—within and between the populations.

a) Clausen et al. studied an alpine and a foothill ecotype of *Potentilla glandulosa*, in California. They distinguished 14 differences. All of these show multiple factor segregation.

b) In two subspecies (or species?) of goldenrods Charles and Goodwin found a minimum of 21 different loci involved in leaf differences, and a minimum estimate for all morphological differences of 40 loci. There is no knowledge of how far the minimum estimate is removed from the actual state.

c) In the poppy *Papaver alpinum* Fabergé shows that many morphological differences between so-called species—better members of a Rassenkreis—are based on single factor differences. It seems that some of the forms differ primarily in one locus only.

3. Differences between closely related species.

a) In *Drosophila virilis* and *D. americana* 12 morphological and 6 physiological characters are recognized as different. Each of these differences depends on multiple genes, but it is not known how many phenotypic differences are due to the same genic differences.

b) *Drosophila melanogaster* and *simulans* differ cytologically—as studied in the $\pm$ paired giant chromosomes of the sterile hybrid—in at least 25 sections or points.

Our ignorance does not give us data as to the relative number of genetic differences underlying the visible differences between individuals, populations, subspecies and related species. It is safe to assume, that on the average differences of individuals belonging to partially isolated groups [4|5] are based on more genes than within an interbreeding group and that differences between individuals of completely isolated groups are based on still more gene differences. There is no doubt that gene differences due to randomness of mutations, drift, differences in selective action etc., would rapidly accumulate, as soon as isolation has occurred genetically or non-genetically.

4. The origin of genetic isolation.

Your question regarding the number of gene differences between related species springs from your interest in the origin of genetic isolation. The statements under (1) and (2) of this letter show that multiplicity of

genetic differences does not necessarily involve exclusion from interbreeding. This exclusion will be due either to accumulation of many differences which then “happen” to be isolating differences or the genetic isolation will be an early phenomenon which, once a fact, permits the accumulation of differences. The first alternative makes a non-genetic isolation of populations a prerequisite of speciation since not enough gene differences could accumulate in two populations which can exchange their genes. This is your allopatric speciation. Even the second alternative often will depend on allopatric phenomena since the formation of two genetically different populations whose genetic differences determine immediately their mutual isolation will be easy if a non-genic barrier keeps them initially from exchanging the relevant genes.

Not because I am convinced of the existence of sympatric speciation but rather because I am not yet sure of its non-existence do I submit the following possibilities.

a) Non-genetic sympatric isolation.

If individuals which due to non-genetic causes happen to occupy a different ecological niche from that of the rest of the population should tend to mate preferably with others of the same niche, an accumulation of genes may result which turns out to be isolational. Of course, this example is nearly identical with “island isolation”. A really new principle would be [5][6] involved if the ecological peculiarity by non-genetic means would condition them for mating between these ecological isolates, including a conditioning of the F_1 for the ecological niche (e.g. the artificial, imperfect case of peppermint oil *Drosophila*).⁹⁸

b) Genetic sympatric isolation.

It is well known that a dominant mutant $\underline{A}$ determining isolation from $\underline{aa}$ will, by definition, eliminate its bearer from evolutionary consideration as it will not produce offspring with the $\underline{aa}$ which form the rest of the population. On the other hand a recessive mutant $\underline{a}$ is conceivable which is carried in heterozygous form $\underline{Aa}$ by many individuals and which homozygous ($\underline{aa}$), isolated from $\underline{AA}$ and $\underline{Aa}$, still will find sufficient $\underline{aa}$ mates. It is true that the $\underline{aa}$ population would obtain an inflow of genes of the $\underline{AA}, \underline{Aa}$ population through its $\underline{aa}$ segregates. However no “backflow” from $\underline{aa}$ to $\underline{AA}, \underline{Aa}$ is possible thus permitting differentiation (“one way isolation”). I do not know of any proven case of such simplicity but is it impossible? I could imagine $\underline{aa}$ to determine ethological properties or temporal isolation even in higher organisms. I can think of it easier in terms of marine or freshwater organisms with external fertilization. We know that spawning, gametic reactions and fertilization depend on activating substances (*Chlamydomonas*, *Hydractinia*, oyster). We know at least in *Chlamydomonas* that different genetic strains react to different activators. If $\underline{A}$ (haploid) makes the

98. This unclear syntax is in the original *Bulletin*.

gametes reactive in one environment, *a* in another, we have sympatric genetic isolation. Similarly if assumed *AA, Aa* *Hydractinia* produce a stuff (1) which leads to spawning 1 hour after dawn while *aa* produces a stuff (2) leading to spawning 2 hours after dawn you have a scheme for sympatric isolation.

I know that Muller has discussed such possibilities and regards them as very remote. Though I think his arguments do carry much weight I bring these possibilities up again, since I think they merit still more discussion.

Here is a question to the paleontologists. Are there restricted [6|7] regions, as for instance former inland lakes, in which successive layers contain *increased* numbers of probably true (isolated) related species? Or are there similar cases in restricted marine deposits giving not a succession of forms but splitting up into various new species—coelenterates, echinoderms, brachiopods, mollusks? If such cases are not known though sufficient opportunities to find them have occurred then a good case against sympatric speciation can be made. If they are known, would you admit them as evidence for sympatric speciation?

Sincerely yours,
Curt Stern

May 2, 1944

Dear Dr. Caster:

In your work with fossil invertebrates you have undoubtedly encountered evidence for or against the statement (frequently made by zoologists) that the paleontologic record has far fewer examples of intergrades which bridge the major categories (link-forms between subphyla, classes, and orders) than it should have if evolution progresses by small increments. It is argued that the rarity of these microgenetic chains throws the evidence in favor of macrogenesis or large systematic mutations, profound morphologic alterations.

Vertebrate paleontological evidence emphatically supports microgenesis in that the morphologic gaps are invariably smaller in the more completely known phylogenetic lines. Unfortunately, this fact has not been adequately expressed, and the situation is, of course, complicated by the inadequacies and ambiguities of the terms we use in trying to say what we mean.

I hope you will be willing to make a statement on this subject.

Sincerely yours,
Glenn L. Jepsen [7|8]

May 9, 1944

Dear Dr. Jepsen:

The aspects of paleontologic discontinuity of which you enquire are matters of great interest to me. What I know of invertebrate paleontology would lead me to support your vertebrate-derived views. "Macro-genesis" has been postulated largely under the compulsion of ignorance. It becomes less and less necessary as the field of paleontologic knowledge increases. I'm afraid I have little sympathy for philosophies or "working hypotheses" of despair. In paleontology it seems to me that we are at best on the threshold of understanding, that the main body of data is yet to be mined, and that it would be hazardous in the extreme for any of us to make sweeping biologic generalizations from our fragmental knowledge which counter those of neontology.

In the grand sweep of paleontologic history the evidence of intimate organic continuity is inescapable. The systematic lacunae seem to be almost wholly correlatable with the physical incompleteness of the fossil record, rather than with any obscure cryptogenic factor or masking attribute of "macro-evolution". Uniformitarianism seems fully as applicable to biology as geology: current biotic phenomena are as much a guide to antiquity as the fossil past is a key to the living present. This does not imply that all existing factors are completely understood, or that the mechanics of evolution are an open book.

The larger the hiatus in animal phylogenies, the greater the correlatable interlude of unrecorded, or incompletely recorded, time, seems to be a constant paleontologic principle. All animal phyla were almost certainly established in the billion years of maritime evolution prior to the Cambrian initiation of the general hard-parts record. Paleontology can therefore hardly be expected to yield absolute interphyletic links. Fossil clues, when coupled with neontologic data of embryology and morphology do make *philosophical* linkage both feasible and convincing. In virtually all lesser [89] biotic hiatuses, less of philosophy and more of fossil fact is employable.

Most subphyla, classes and orders seem to have been generated in the long, unrecorded junctures between the registered eras of history; similarly, the origins of subordinate major categories commonly correlates with inter-system or -series breaks. Probably the majority of new genera appear at the nonconformable inception of new stages or formations and within the confines of these stratic units the aggregate changes noted are ordinarily specific or sub-specific (varietal, mutational, "Waa-genal",⁹⁹ etc.). Even here it is likely that the diastemata (bedding-plane

99. Caster added a footnote to the original text in this spot, reading: "A fair solution to the homonymous usage of the term *mutation* by geneticists and paleontologists must yield to the geneticists and introduce a new paleontologic term. Since the latter usage dates from the work of Waagen, it is suggested that the paleontologic "mutants" be henceforth known as *Waa-gens* (germanic pronunciation), and that the adjectival and adverbial forms 'waagenic' and 'waage-nal' be employed where needed."

interruptions in record) within almost any sedimentary unit attest more absolute time than the deposit itself. In most cases we observe summations (*Waagens*) of slow change, rather than true genetic mutation.

In rare circumstances, exceptional fossil conditions preserve somewhat more of the mutative and selective data than is the general rule. Fenton has illustrated such circumstances among Paleozoic spiriferid brachiopods in a single marine environment and horizon. A stereographic glimpse of this phenomenon as it progressed through time and in several adjacent marine environments has been the subject of considerable study in connection with my own work on late Devonian and early Mississippian Pelecypoda. The setting lies in the Penn-York Embayment of the Appalachian Plateau where several hundred feet of delta beds were built out into a narrow gulf over a period of probably several million years. Concentric with the strand, several benthonic facies (fossil [9][10] environments) continued to exist and while the strand-line was progressively forced westward toward the open epeiric sea. On the basis of detailed morphologic comparisons and detailed stratigraphic correlation, it has been possible *to interpret* certain changes which took place as geographic (environmental or adaptive) sub-speciation, inter-facial migrants, intra-facial “waagenations”, and possibly as homofacial mutants. These rare recordings seem to be evidence of “micro-evolution” in normal operation.

So many destructive factors were operative against the fossil record and so much change occurred in circumscribed areas forever lost to us, during the five hundred million years of the Phanerozoic, that the marvel constantly is not how *little*, but how *much* has been preserved. It is significant that we catch no glimpses of catastrophic change of “macro-evolution” in the *record*. These events are almost consistently postulated for the *non-recorded* interludes or *unknown* recesses. Moreover, it seems to me that essentially every time—or environmental—break in sedimentary history uncompasses [*sic*] *adequate* time for the slow, blind, mutative and selective forces of “micro-evolution” to produce the encountered organic alteration.

Yours sincerely,
Kenneth E. Caster

May 4, 1944

Dear Mayr:

Paleontology presents good evidence, as you know, that evolution proceeds by microgenetic rather than by macrogenetic alterations, and this evidence is in harmony with experimental genetics.

There are many examples of the fact that, in general, the more completely known phylogenies have fewer and smaller “gaps” in them; the less-well-known sequences have more and larger “morphologic breaks”.

The evidences for genetic sequences in these phylogenies are almost wholly morphologic, based primarily (in most instances exclusively) upon the hard parts. Necessarily the [10|11] only practicable method of classifying fossils is founded upon morphology.

If, however, we had the complete evolutionary record (morphologic expression of a linear or “vertical” genetic continuum) of a group, we could not manufacture categorical boundaries between constituent sub-groups or between individuals by any morphologic or genetic or other criteria currently employed.

How do the systematists propose to handle this situation?

Neontologists frequently avoid the issue or elaborate it to incomprehension by making one or more of the following assertions: (1) it is up to the paleontologists to devise their own system of taxonomy; (2) it is necessary or desirable to use different taxonomic systems for fossils and for living forms; (3) the “gaps” in the phylogenetic records adequately do and can continue to provide convenient negative evidences for positive uses as “discontinuities”; (4) less is to be gained by further study of morphology than by seeking new non-morphologic bases for classification.

Each of these implies attitudes which, when they are expressed in taxonomy, are conducive to disunity and disharmony in taxonomic practices; they all obviate consideration of systematics as a distinct discipline or established technique.

This letter is addressed to you because you have become familiar, in your work with many of the difficult problems which are involved in the consideration of “horizontal” versus “vertical” discontinuities.

Sincerely yours,
Glenn L. Jepsen

May 22, 1944

Dear Jepsen:

Your question concerning the nomenclatorial treatment of completely connected series of vertical forms poses a real problem. Its solution can not be attempted without a short survey of the history of taxonomic categories nor without a discussion of similar difficulties of the neontologist, the student [11|12] of living species.

Linnaean taxonomy was essentially no-dimensional, that is it dealt with the delimitation of natural population at a single locality and at a single time level. Subspecies are absent (by definition!) under such circumstances and it is therefore nearly always simple to determine the species limits of sympatric and synchronic species. The scientific exploration of the whole world in the post-linnaean period resulted in the addition of longitude and latitude to the domaine [*sic*] of the taxonomist.

Taxonomy thus became two-dimensional and it became necessary to replace the simple species of Linnaeus by the polytypic species of recent authors. This has led to complications which have not yet been entirely overcome and some of which probably will never be overcome. Three major difficulties of the neontologists come to my mind: (1) How to delimit subspecies which intergrade insensibly, and what names to apply to intermediate populations?, (2) How to treat geographically isolated populations (whether to call them species of [*sic*: or] subspecies)?, and (3) How to treat those borderline cases, where populations of the same species act like subspecies in parts of the range, and like different species in other parts? To be quite frank, I believe that a completely satisfactory answer is impossible in all such cases, because evolution can not be made to fit perfectly into the artificial, man-made frame of nomenclature. At best, we can reach a poor approximation in our nomenclature.

Life is spread over the earth as a thin film and the dimension of space does not seem to provide any taxonomic complications except possibly in the ocean and in deep lakes. Time, however, is a dimension of fundamental importance to the paleontologist. The paleontologist deals with vertical sequences in addition to horizontal ones. This poses an entirely new set of problems, problems which were more or less ignored so long as the fossil record was fragmentary. However, in recent years the knowledge of many fossil lineages has reached such a degree of completeness that a practical solution [12|13] of a number of problems becomes a necessity. As I see it, the various problems can be grouped under two basic questions: (1) Where should the cut be made between chronologically adjacent species particularly when an uninterrupted vertical sequence of fossils is available? (2) Is it desirable to make a terminological distinction between horizontal and vertical subspecies, and if this question is answered in the affirmative, how can this distinction be expressed in our nomenclature?

Ad (1). As far as the first of these two problems is concerned, it seems to me that no real solution is possible, if one believes in gradual evolution, rather than in macrogenesis. We might as well accept the fact that in nature there are no borders between vertical species of the same lineage. Whatever species the taxonomist recognizes within such continuous lines are merely convenient aggregates around artificial focal points. These focal points consist usually of the earliest found fossils. It is to be understood clearly that in such cases chronologically adjacent populations of two different species are much closer to each other than they are to other populations of the same species. To make this point clear we might illustrate it in [an] imaginary example. Let us assume that we have the complete fossil record of a lineage which changes very gradually through 25 arbitrarily delimited successive time-levels (strata), calling the lowest or earliest stratum level 1. This lineage was first discovered in level 18 and names [*sic*: named] species *a*. It was later

found in stratum 5 and named species [*sic*: species] *b*. At a still later date additional fossils were found in the missing 23 strata from 1 to 25, until the complete series was established. The point is that the fossils from strata 1–4 and from 6–11 are too similar to species *b* (from stratum 5), and the fossils from strata 12–17 and from 19–25 too similar to species *a* (from stratum 18) to justify their description as separate species. In consequence the fossils of strata 1–11 are recorded under the name of species *b* and the fossils of strata 12–25 are recorded under the name of species *a*. This is done [13|14] and has to be done, notwithstanding the fact that some populations of species *a* (e.g. those of stratum 12) are more similar to some populations of species *b* (e.g. those of stratum 11) than to other populations of species *a* (e.g. strata 18–25). I can not see how we can avoid this paradoxical decision. Incidentally, Simpson ([Simpson 1943], p. 172) comes exactly to the same conclusion. The recognition of vertical subspecies within each of these species helps, of course, to bridge the gap between one species and the next. As mentioned above, the neontologist often must make a similar arbitrary decision when he delimits subspecies.

Ad. (2) The question of a terminological distinction between vertical and horizontal subspecies is more involved. Simpson, whose excellent discussion on this subject should be consulted by every student ([Simpson 1943] p. 168–177) used exactly the same nomenclature for vertical (allochronic) subspecies as for horizontal ones (sy[n]chronic-allopatric). This may be adequate terminology when there is no danger of confusion between horizontal and vertical subspecies. The subspecies in the conventional papers of the ornithologist are always horizontal. The subspecies (if used at all) of the student of early Tertiary mammals or of Mesozoic fossils are always vertical. However, in the field of Pleistocene paleontology difficulties are conceivable, in fact they have already arisen. Weidenreich, for example, in his studies on the phylogeny of early man in southeastern Asia has been up against exactly this difficulty. He finds in Java approximately the following phylogenetic sequence (beginning with the most recent form): *Homo sapiens australicus*, *Homo sapiens wadjakensis*, *Homo (Javanthropus) soloensis*, *Pithecanthropus erectus*, *Pithecanthropus robustus*, *Meganthropus palaeojavanicus*, preceded in continental southeastern Asia by *Gigantopithecus blacki*. Translated into the nomenclature of recent taxonomy this series would probably be called: *Homo sapiens australicus*, *H.s. wadjakensis*, *Homo erectus soloensis*, *H.e. erectus*, *H.e. robustus*, *H. palaeojavanicus*, and *Gigantopithecus blacki*. [14|15] This is an unbroken lineage in which each step might well overlap the two neighboring ones if sufficient material were available to show the full width of variability.¹⁰⁰ The differences between neighboring categories are

100. Mayr developed this thinking further in Mayr (1951; 1963).

sufficiently slight in each case to indicate that interbreeding would have probably taken place, if the populations had met at the same locality and time level. In other words, each of the above listed steps is only subspecifically distinct from its neighbor above and below. The gap between the early giant type and *Trinil* Man is closed by *H. palaeojavanicus*, and that between *Trinil* Man (*erectus*) and modern man is bridged by *soloensis*. In other words, disregarding a number of uncertainties, we have here a continuous series of subspecies, of which the end links are certainly different enough to be considered as reproductively isolated, in fact which are so distinct that it is advisable for the time being to split the entire series into 3 or 4 species. As long as we restrict our attention to Java, matters are relatively simple. However there is a parallel line on the Asiatic mainland, much more poorly known at the present time, but characterized (beginning with the oldest) by three major steps: *Gigantopithecus* (possibly common ancestor with the Java line), *Homo erectus pekinensis*, and *Homo sapiens mongoloideus*. The striking parallelism in the evolution of the two lines indicates that they are not to be considered as completely isolated from each other, but rather as having sufficient continuity through connecting populations to insure a continuous gene exchange. In the Asiatic mainland line, *H.e. pekinensis* is so similar to *H.e. erectus* from Java that they must be considered as horizontal subspecies (assuming approximate contemporaneity) of the same species. Likewise the modern Mongolian race (*H. sapiens mongoloideus*) is considered only subspecifically distinct from the modern Australian aboriginal (*H. sapiens australicus*). We thus have a clearly developed system of horizontal and vertical subspecies in *Homo* of eastern Asia and the adjacent Sunda Islands. It is at once evident that it is desirable to express that *pekinensis* is a geographical representative [15|16] of *erectus* (allopatric, synchronic) while *soloensis* is a younger descendant of *erectus* (sympatric, allochronic). In view of the overwhelming usage of subspecies in neontology (as compared to paleontology) it would seem most practical to continue the use of simple trinomials for synchronic, geographical races (allopatric subspecies). Some special affix, suffix or other sign would seem desirable for vertical subspecies. For example one might write: *H. erectus erectus*, and *H. erectus pekinensis*, but *H. erectus-soloensis*, or *H. erectus post-soloensis*, or *H. erectus-p-soloensis*.

It seems to me that it will be up to a committee for nomenclature in paleontology to adopt a definite terminology. However, it might be advisable to have first an experimental period, during which various schemes are tried, before a formal and final ruling is made.

There is one point which needs to be stressed in this connection: It will never be possible, not even by the most finely elaborated nomenclature, to express exact relationships and degrees of difference. This is true in neontology, and to an even greater degree in paleontology. For

example, if an early Neandertaloid form of the “*Sinanthropus*” series should be discovered, it would be a horizontal subspecies of *H.e. soloensis*, and a vertical subspecies *H.e. pekinensis*. I do not quite see, how this could be expressed by any symbols. In fact, it would be very cumbersome if one would introduce symbols to express all these fine nuances of relationship. The specialist does not need them and the outsider would not understand them.

To summarize this discussion I would suggest that paleontologists use a vertical bar or some other symbol to indicate vertical races, but not to make a formal ruling until such a system has survived a trial test.

Sincerely yours,
E. Mayr [16|17]

May 14, 1944

Dear Dobzhansky:

“Suppose that an intelligent anti-evolutionist should assert that the information available proves that the evolution of higher plants has ceased since the end of the Cretaceous. What evidence can one oppose to such an assertion?”¹⁰¹

Your question is more sweeping than Chaney’s statement which I assume prompted it, namely, “My present opinion is that since the Cretaceous period the *forest* vegetation of the *tropics* has been *relatively stable* as to species.” (my [Epling’s] italics). An assertion as sweeping as the one you suggest would be rash indeed; yet, if made, I believe a convincing answer might be returned. This answer would be based on inference, of course.

Our knowledge of Eocene floras is confined to a relatively small sample of forest species. This sample indicates that very little change in form has taken place in the plants represented and that, if not conspecific with modern species, they are very similar and, if living, might very well be members of the same species group. This indication is still convincing despite that [*sic*: the] fact that a given fossil which in this decade may be referred to a certain genus and family, may in the next be referred to another genus or family, sometimes quite remote in the system. It gains in probability because many of these Eocene fossils are associated in time and space in a way that recalls present day communities of the species which they resemble, an association which is not only qualitative but quantitative [*sic*] to some extent. Resemblance’s [*sic*] of isolated individuals might be ascribed to chance or to parallel evolution, but such associations lend weight to the probability of genetic continuity.

101. Dobzhansky posed this question in his 14 April 1944 letter to Chaney in *Bulletin* 1.

Let it be granted, however, that forest species of the types represented in the Eocene have undergone little or no evolution since that time. They still represent only a small proportion of extant species and represent only one vegetative type. The great mass of vegetation not only of [17|18] temperate regions but also of the tropics is comprised of semi-woody or herbaceous types. These types are generally believed by botanists to have been derived from woody types. Have they originated since the Eocene? Do they give evidence of active evolution? The fossil record tells us very little because the leaves of herbaceous and semi-woody plants are not fitted for preservation, or so it is believed, and it is true that they are absent even from Pleistocene floras where their presence in the vicinity seems scarcely to be doubted. In the absence of any records we can only infer their presence or absence by two lines of reasoning which are suggested by the following questions. May the climate of the Eocene have been sufficiently diversified to accommodate communities of herbs or shrubs, such as are now found in the savannas and shrublands of the tropics? In view of part topographic changes, may we infer from present distributions of herbaceous groups whether they may have been present in the Eocene? If present, may we infer from their modern distributions whether evolution has taken place since?

What of Eocene climate? We are told that the supposed tropical equivalents of the Eocene fossils exist today in communities and in reaction to climates in which herbaceous vegetation is largely excluded or, if present, is of weedy nature, except the highly specialized epiphytes such as Bromeliads and Orchids. Because we believe that certain leaf types represent an adaptation to such climates, and because the Eocene fossils are preponderantly of this type we infer therefrom a similar climate at the time and place they were deposited. I believe we are justified in this inference. From this inference and from geological facts a relatively low relief during the Eocene is inferred and, as Chaney has pointed out, a movement northward of the isoflors to a point which permitted a supposedly wet subtropical forest to flourish as far north as the coasts of California and Oregon. From the floras of the interior is inferred a more continental but still humid upland. But all of these deposits are from the higher latitudes. No records exist for the lower latitudes. Now, [18|19] if the basic facts of meteorology be taken into account, and if, as seems probable, the outline of the continents has not changed materially during the Cenozoic, then it can scarcely be doubted that a belt of relative aridity existed somewhere in the middle latitudes even then. This belt is sharply defined at present, but its intensity during the Eocene need not have been more than enough to produce an alternation of "wet" and "dry" seasons to provide conditions in which tropical savanna and shrubland might have developed. That such an arid belt existed and had produced a corresponding reaction in the vegetation of the Eocene is suggested by the appearance in the Florissant [*sic*: Floris-

sant] of shrubby elements of the north Mexican vegetation (an arid subtropical type) as pointed out by MacGinitie. Furthermore, Chaney has recently found in the Green River what appears to be an *Opuntia*. This find would clearly indicate to me the presence of a semi-woody type specialized, not necessarily to desert conditions but at least to recurrent periods of drought for many present day cacti, although able to withstand long periods of dessication [*sic*], are nevertheless tolerant of continually moist soil, provided that the drainage is good. Some, such as the epiphyllums and similar genera do not require direct sunlight, but, at least in our region, thrive best in its absence, flower, and set seed. *Pachycereus* exists on the Viscaino desert in an atmosphere sufficiently humid that it festooned with *Tillandsia*. I believe it not only possible, but also probable that some Eocene climates may have supported shrublands and in view of the Eocene *Opuntia*, even a cactus savanna of the type which now exists in Venezuela.

The woody families and genera which characterize the Eocene floras are generally found at present in both hemispheres. But if one examines the present distribution of *Angiosperm* families which are herbaceous or semi-woody he is struck by the fact that some, like Bromeliaceae or Cactaceae, are confined to one hemisphere. Still others, as Orchidaceae, may occur widely in both hemispheres, but within the family related groups of genera have either [19|20] a neo- or a paleotropic distribution. This fact suggests the possibility that such families may have originated and persisted in one hemisphere only and may accordingly be relatively recent in origin and diversification, although such an inference does not necessarily follow. However, if one examines the distribution of the larger genera of such admittedly primitive families as *Ranunculaceae* in the *Dicotyledons* and *Alismataceae* in the *Monocotyledons*, he is struck by the very wide distributions which characterize them. For example, of *Ranunculaceae*, the larger genera *Caltha*, *Anemone*, *Clematis*, *Myosurus* and *Ranunculus* occur in both hemispheres, including Australia, South Africa and New Zealand, save for *Myosurus* and *Caltha* which are absent from South Africa and *Anemone* which is absent from New Zealand. The closely related family *Alismataceae* has a similiar [*sic*] but somewhat more restricted distribution. Moreover, it is perhaps pertinent to our discussion to note that the genus *Ranalisma*, which strongly suggests *Ranunculus* in some respects, is endemic to wet tropical forests in the Malay Peninsula and West Africa. These distributions suggest great antiquity (and, if any weight can be attached to *Ranalisma*, a tropical origin).

What may one infer from the present distribution of an advanced herbaceous or semi-woody family which is also widely spread? The *Labiatae* with which I am relatively familiar can be taken for discussion. This family is large and diversified; it is ubiquitous in all parts of the world, but is mainly tropical or subtropical.

In the tropics it forms an important constituent of shrublands and savanna, either of the plateaus, as in the case of the large and well defined genus *Hyptis*, or of the intermediate mountain slopes, as is the case of the large and equally well defined genus *Salvia*. The genera or generic groups of *Labiatae* are found principally in one hemisphere or the other. Exceptions occur however, which I shall mention later. The growth form of *Labiatae* is predominantly shrubby, with relatively small, non leathery leaves, but many genera are strictly herbaceous. Genuine tree forms are few and may be limited to the genus [20|21] *Hyptis*. Such trees are small, but have relatively large, entire and tough leaves, although they are not of the “forest” type. It is perhaps pertinent that the best defined of these, *H. arborea*, occurs in the ancient flora of Mt. Roraima, jumps to Colombia and thence to Bolivia.

The distributions of *Hyptis* and *Salvia* may be taken as illustrative of the generic distribution of most of the family. *Hyptis* is neotropic, but is closely allied to a generic complex of the old world. These two groups appear therefore to have evolved independently, for in two groups of similar growth form and requirements and widely distributed, one might reasonably expect the present association of at least a few species of one or the other, if they originally occupied the same territory. *Salvia*, on the other hand, is found in the mountain masses of both hemispheres and occurs also in South Africa and in Australia, but the great mass of the genus, the subgenus *Calosphace*, comprising more than 500 species, is wholly American, and like *Hyptis*, appears to have evolved independently of the old world groups.

These distributions are typical of the family, and it is reasonable to believe that these large phylads, and hence a large part of the family, have evolved independently since the two hemispheres were separated floristically. But other distribution patterns similar to those of the primitive families mentioned are also found. For example, the genus *Lepechinia* which, like *Salvia* is principally cordilleran in the new world, resembles that genus in habit. It is shrubby or herbaceous. It is clearly defined by reason of its nutlets which are unique in the family. It ranges from California through the Mexican highlands and the Andes to Chile and Argentina. It also occurs in the mountains of east central Brasil, in Haiti (an area of high endemism in *Salvia*), in Baja California, on Socorro Island (Revillagigedo) on Maui of the Hawaiian group, and on Reunion Island. The species found in Baja California and on Maui is sharply defined and suggests the Brazilian species. That of Haiti is more closely allied to certain of the Andean species. [21|22] The species on Reunion Island, which, it is true, is known from a single specimen, is similar to one in Chile, but both are distinctive in habit and foliage.

The genus *Scutellaria*, together with a monotypic genus of the southwestern United States, is sharply defined by its peculiar nutlets and their mode of attachment. It is herbaceous or at most subshrubby. It is world

wide in distribution. One of the most specialized groups is the section *Galericularia*. It is strictly herbaceous, with creeping rhizomes, a dweller in moist soil. This section ranges throughout North America and Eurasia, including Yunnan and Japan; one distinctive species which is closer to those of Europe than to those of North America, occurs in tropical America from Mexico to Argentina, and one species occurs in Australia.

The genus *Stachys* is also strictly herbaceous. One species group particularly deserves our attention. The greater part of this section is cordilleran, ranging from the Cascade Mountains to Colombia. Three species pairs have a striking distribution. One species which occurs in central Mexico is paired with one in the Cape Region of South Africa. A second which occurs in Peru has a close counterpart in a species of [*sic*: in] Yunnan. A second Mexican species is so closely similar to a species of [*sic*: in] Uganda that they might readily pass as the same if found in one herbarium folder, not merely in technical characters but in that summation of imponderables so familiar to systematists.

The genus *Teucrium* is an herbaceous or sometimes shrubby genus which is represented in the new world by two species groups which differ markedly in growth form. Of these, the first ranges throughout North and South America, including a species on Haiti and another in the Galapagos Islands. It also ranges in Eurasia to China and Japan, to the East Indies and to Australia. The second species group is found in the southwestern United States and arid Mexico, and throughout the Caribbean Islands. Restricted endemics occur in California, on Clairon [*sic*: Clarion] Island (Revillagigedo) and Cedros Island. The group reappears in [22|23] Argentina and two restricted species occur in Chile. In the old world, it is found in the Mediterranean, at the Cape of Good Hope and in Australia.

As a final example I shall mention what appears to be a polytypic species of *Agastache*, another herbaceous genus. *A. scrophulariaefolia* occurs widely in the eastern United States, and exhibits two forms which are not segregated very sharply. Its western counterpart is *A. urticifolia*. The single species of the genus found in the Old World is *A. rugosa*, widely spread from Manchuria and Japan to Formosa and Yunnan. This species is scarcely separable from one of the two forms of the eastern United States.

One can do no more than speculate upon the antiquity of these distributions. Assuredly they are not recent. Such distributions as those between Haiti and the Andes, as in *Lepechinia* (and numerous examples in *Salvia*, or between the Isle of Pines and central Brasil, as in *Hyptis* and *Eriope*, or between the Antilles and the Galapagos group, as in *Salvia*) seemingly cannot be later than early Cenozoic, in view of the conjectured history of the Antillean region. Relationships such as those between the Americas, South Africa and Australia, as in *Teucrium* and *Stachys*, must be equally or more ancient. I myself believe that they may

be Cretaceous. In any event, it seems probable to me that the Labiatae were well differentiated as to genera and subgenera and widely distributed by the Eocene and, in view of their importance today in tropical shrubland and campo, it seems reasonable to believe that they were a part of whatever Eocene vegetation was characterized by a fairly sharp differentiation of wet and dry seasons.

Inasmuch as the Labiatae are generally recognized as the most advanced family of one of the principal phylads of Angiosperms, this conclusion might be taken as an indication that evolution in the Angiosperms has been stagnant during the Cenozoic. However, evidence such as that advanced by Professor Babcock indicates that evolution has progressed during this period by fragmentation of polytypic species as well as through ploidy, and the [23|24] distribution pattern of most of the family suggests a similar evolution and diversification. Nevertheless, it does appear as though relatively little evolution of *form* has taken place during the Cenozoic. Most of our orders and families, many of our familiar genera and even some of our species appear to have great antiquity. It seems to me that the main outline of the Angiosperm pattern was probably fixed by the beginning of the Cenozoic, as suggested by the known fossils and the distributions of living groups. The changes which have occurred since seem to be principally recombinations or variations of its details. This seeming truth may also apply to other phyla. More than one student of the amber insects has found little or nothing to differentiate them from those of the present. On the other hand, the fossil record during this period bears testimony to the rise, differentiation and disappearance of whole orders of land vertebrates. Perhaps the seeming diversity of these forms is enhanced by the nature of vertebrate taxonomy. Even so, the fact remains that a remarkable change of *form* has taken place. But this was the point on which I asked your comment.

I shall summarize these considerations as follows. I believe that, although relatively little change in form may have characterized the Angiosperms during the Cenozoic, species formation is not thereby precluded, particularly amongst herbaceous and shrubby groups which have entered an expanding environment, because of the grand cycle of increasing aridity since the Oligocene. Why Angiosperm form should have changed so little, in comparison with the vertebrates, I leave for your speculations.

Sincerely yours,
Carl Epling

May 18, 1944

Dear Dobzhansky:

A) You ask whether the plant kingdom furnishes many good polytypic species in which the extreme subspecies differ morphologically about

as much as do [24|25] sympatric species of the same genus, excluding polyploidy and other aberrations.¹⁰²

I am limited in replying to this question because of a lack of knowledge of chromosome numbers in the groups with which I have dealt by the herbarium method. I can only say with regard to them that the pattern of variation differs in different genera and species groups. In some the entities, whatever they may be, are sharply differentiated morphologically and may or may not be sympatric. The *Salvias* you mention, meaning in this instance the subgenus *Audibertia*, are examples. Most, if not all, of the species have the same chromosome number ($2N = 30$) and show no polyploids. They show no "inter-gradation" as a botanical systematist understands this term. Only one of the species shows marked geographic differentiation and this, *S. carnos**a*, which ranges from northeastern Washington to central Arizona, may be taken as a polytypic species. In other genera, the supposed species may be less well marked. In either case, most genera or species groups which embrace several species usually exhibit one or more such polytypic complexes. The fact that the differences between the 'species' of a species group, whether they be polytypic or homogeneous, are about of the same order of magnitude, and the fact that some of these species are usually sympatric to some degree or other, suggests that they are in fact species. Two other polytypic species which occur to me, in which the chromosome number is known are *Pinus ponderosa* and *P. contorta* [*sic: contorta*], which show marked geographic differentiation over fairly wide specific areas. Their geographic races intergrade. But side by side with such species exist other series of allopatric forms which, although very similar, do not intergrade. The five needle pines may be taken as an example: *Pinus excelsa* occurs in central Europe. *P. Strobus* occurs in the northeastern United States. Closely paired with it is *P. monticola* which ranges from British Columbia and Idaho into the Sierra Nevada. In much of that range *P. monticola* comes into contact with *P. albicaulis*, a subalpine species. In Oregon and California, it meets *P. Lambertiana* at its lower margin. In southern [25|26] California, *P. Lambertiana* comes into contact with *P. flexilis*, and finally in Mexico occurs *P. Ayacahuite*. Here then is a series of closely related forms, which are allopatric, either remotely or connectent [*sic: connected*]. The layman might find difficulty in recognizing at least the immature stages of each. Yet, although several of the species actually intermingle in some areas, neither botanists nor foresters are in doubt of their constancy and specific identity. I am myself familiar with some of these intermixtures in both Idaho and California and have never observed any "intergrades." Viewing a distribution pattern of this kind, particularly if the areas were somewhat more insular than in this instance, I suspect that some zoologists might consider

102. Dobzhansky posed this question in his 14 April 1944 letter to Chaney in *Bulletin* 1.

the whole group a species. Botanists generally accord each segregate specific rank.

As a similar example, I might cite a geographic complex in *Delphinium* on which Harlan Lewis and I have been working. Disregarding two tetraploid forms which do not affect the illustration I wish to make, the whole complex is diploid (2M [*sic*: 2N] = 16). From the morphology and distribution of the complex, I believe ornithologists might call it a polytypic species. Samples from a colony of each of the most [*sic*: most] extreme forms, whether living or preserved would be indeterminable if they consisted only of the inflorescence. If the basal leaves should be included two categories would be distinguished by virtue of the differences in lobing and pubescence. Even so, some individuals might be determined with difficulty by a systematist not familiar with the genus. But if the seeds should be included, even a layman could distinguish them. I shall call one *D. Hanseni* and the other *D. hesperium*.

D. Hanseni is confined to the foothills of the Sierra Nevada, save that it crosses the Sacramento Valley into Yolo and perhaps into Contra Costa Counties. It is segregated into two fairly well defined geographic races. At generally higher elevations in the oak woodland, a blue flowered race ranges from Kern County northward to Butte County. This is further differentiated into less well defined northern and southern pubescence forms. At lower [26|27] elevations, at the lower margin of the woodland and extending onto the treeless foothills is a white flowered race which ranges from Kern County northward to Mariposa County. It, too, exhibits the same pubescence forms, but they are less clearly segregated geographically. Where it occurs on the western side of the Great Valley, *D. Hanseni* comes into contact with *D. hesperium* to an ascertained distance of five miles and perhaps less. No mixed colonies are known.

D. hesperium occupies the Coast Ranges. Like *D. Hanseni* it exists as two races, blue flowered and white or pale. These races are also different in other less tangible ways. The blue flowered race ranges along the coast from Monterey Bay to Humboldt County. In the north it has a different facies, hardly definable. The white flowered race ranges in the warmer drier interior valleys from San Luis Obispo County to Glenn County. It is this form which comes into contact with *D. Hanseni* in Yolo County. Within each species the races intergrade and flowers of intermediate color are found in the intermediate areas. We have F₁ plants of these races, variously combined, and F₂ plants as yet immature. Hence the fertility is undetermined. In view of other instances in *Delphinium*, some interfertility is expected, but no intergradation between the species is known in nature.

Despite the similarities in form which I have described, the spatial and ecological relationship of the geographic variants and their probable partial fertility, plant systematists have long recognized two species, and

I am inclined to agree with them. Lacking more information as yet, I must illustrate my reasons by reference to *Salvia mellifera* and *S. apiana*. These species are widely different in all parts, so much so that the latter has been employed as the type of a generic segregate. They are partly sympatric and may occur together. Where they occur together frequent hybrids may be found which are probably F_1 s and known to back cross in nature to one parent (and insofar as known probably to one parent only, probably because of the pollinating [27|28*] agent). When selfed in the field these F_1 s give some good seed and the back cross is fertile. Occasional colonies may be found where there seems to be introgression, although nothing like hybrid swarms are known. But because of the spatial relationships of the species, correlated with their extreme differences in form and its constancy, I am inclined to believe that any introgression remains localized for some reason unknown. Despite the partial and perhaps considerable interfertility, the great mass of both species appears to be isolated. If actually true, I believe this isolation may be attributable to factors of the reproductive environment which may reinforce the partial fertility barriers. Such differences in the reproductive environment of plants and animals may provide the basis for an actual difference in species patterns of plants and animals. This leads to my speculations in reply to your fourth question. But before I go on, let me summarize my experience with polytypic species in plants, as I understand them. I believe that they occur in plants, but doubt whether they are as abundant as they are presumed to be in birds. Hence I am inclined to believe that the judgment of plant systematists is frequently correct when they refer similar allopatric forms to specific rank. At the same time, I wonder whether ornithologists have not gone further than they should in constructing polytypic species without more evidence of breeding potentials. After looking over Alden Miller's specimens of *Junco*, rather cursorily, it is true, it seemed to me that had been Labiatae, I would have organized them in much the way that he did. Yet I have heard it suggested that *Junco* is simply one polytype. Knowing what I do of the pattern of variation in Labiatae as a whole, it would assuredly do violence to my sense of proportions, if it should be suggested that the species group of *Salvia* which includes *S. carnosae*, *S. mellifera* and *S. apiana* is no more than one polytype.

B) If species formation via the polytypic species is not very common in higher plants, could one correlate this with the apparent high evolutionary [28|29] conservatism which paleobotanic data seem to indicate?

The fact that relatively few plant species are polytypic, if true, may not necessarily indicate a greater evolutionary conservatism, but rather a difference of isolating factors with respect to the life cycle and the reproductive environment. To a botanist the reproductive environment of at least the warm blooded animals seems remarkably uniform from

species to species and from genus to genus, as compared with plants. Fertilization takes place under similar conditions of moisture and temperature; the embryo develops in an environment which is relatively uniform; the young are not immediately thrust into a hostile world, but receive a varying amount of nurture and guidance, often until they approach sexual maturity. In any event the individual attains a considerable development before it is subjected fully to the vicissitudes of the environment. Hence, a species which had become differentiated into two or more geographic races might persist for a long period as a polytypic species until a marked degree of sterility had been attained, for a large proportion of the young in the intermediate zones has a good chance of surviving and thus maintaining the intermediate population. Or so it seems to a botanist.

I believe that it may be otherwise with plants. In plants the pollen and the ovules are subject to the direct effects of temperature and wilting. The degree of atmospheric humidity may affect the physical condition of the pollen and the opening of the anthers [*sic*: anthers]. The pollen is frequently transported, at least in principal part, by specific agents. Any modification of this relationship will affect fertilization. Once fertilization has taken place the developing embryo is subjected, like the ovules, to temperature changes and to wilting. But more important probably than any of these effects is the apparently narrow range of conditions which must be met in order for the seed to germinate, and, once germinated, for the seedling to establish itself. Once it becomes established, it still must compete for moisture and light until maturity is reached. Once mature, those that survive frequently live for very [29][30] long periods, subject to but little hazard; whereas the animal must continually defend itself from extinction. These critical conditions of pollen transfer, seed germination and seedling establishment, it seems to me, would greatly reinforce any partial sterility which might arise between geographic races and thus produce allopatric species rather than allow the survival of a polytypic species. If true this would explain why the situation illustrated by the white pines is probably more common among seed plants than that illustrated by *P. ponderosa* and *P. contorta*.

Consider, for example, *Salvia apiana* and *S. mellifera*, species which differ strongly in floral structure. The latter is assuredly pollinated in large part by honey bees; I believe, but am not yet certain, that the former is pollinated chiefly by bumble bees. Honey bees rarely visit it, if ever. The F_1 flower of these species is so constructed that honey bees might pollinate it and they are known to visit it. These facts may account for the observed fact that back crosses occur with *S. mellifera*, but seemingly not, or but seldom with *S. apiana*. Here, then, is a partial barrier, which if it does not prevent introgression from *S. apiana* into *S. mellifera*, at least assists in isolating the former. Furthermore, differences in seed germination may also exist. Although the two species may

occur together, *S. mellifera* is predominately coastal, whereas *S. apiana* ranges into the interior, even into the desert community. Where they occur together, *S. apiana* is found in the drier sites. The differences in the numbers of seeds produced by the parent species and any chance hybrid would reduce the chances of any F_2 plants arising, and the chance of a recombination arising and surviving in which the germination equilibrium was not disturbed might be small indeed. These speculations may therefore suggest why no immediate populations exist although the species are interfertile to a considerable degree.

I suggest, summarizing the stated data, that evolution by polytypic species is no less a fact in the Angiosperms than in some animals, but that [30|31] fewer polytypic species and more allopatric cenospecies are actually found in plants (if true) because the great variation in the reproductive environment of plants may serve to reinforce sterility barriers which are only partial, and hence may prevent the formation of intermediate populations which are possible in animal species with a uniform reproductive environment. Perhaps I have neglected other conditions or factors which might produce the same results in animals.

Sincerely yours,
Carl Epling

June 1, 1944

Dear Dr. Mayr¹⁰³:

I was much interested in the exchange of views on "Problems of Genetics, Paleontology and Systematics".

I would like to correct the statement which you make on p. 21 [in *Bulletin* 1], later taken up by Dr. Colbert: "One would expect on the basis of Sewall Wright's formulae—other factors being equal—that rare species evolve more rapidly than abundant ones, also that sedentary species evolve more rapidly than migratory ones". I have frequently been quoted as holding the first part of this statement (notably in Goldschmidt's [1940] *Material Basis of Evolution*, p. 137–138) but it is not a view that I have ever held. Neither have I ever held quite the converse. The general conclusion that I reached has been that evolution depends on a *balance* among the various factors—mutation pressure, selection pressure, immigration pressure and accidents of sampling. This means with respect to numbers (assuming a given situation with respect to these other factors) that there is a certain *optimum* effective population for a neighborhood (group within which there may be considered to be random mating). In any case, the larger the number of such groups in the species the more rapid the evolutionary process may be expected to be

103. The original letter is in Wright Papers, folder "Mayr, Ernst 1944–1951."

(assuming other conditions are such that any evolution at all is to be expected.) [31|32]

With respect to certain types of mutation, notably reciprocal translocations, the optimum for the “neighborhood” is extremely small, a little more than one, or predominant uniparental reproduction. In other cases, the optimum may be relatively large. With a marked secular change in the conditions of life and hence in the direction of selection it would probably be true that immediate progress would be most rapid if the neighborhoods were as large as possible. Even in this case, however, evolution might go farther and reach a more radical solution of the difficulties presented by the changed conditions at some intermediate size of the neighborhood unit, that permits a more rapid and extensive process of trial and error among these than where they are very large.

These considerations obviously imply a similar correction for the second part of your statement. Here again the mathematical theory leads to no sharp decision between sedentary and migratory species. It is a matter of the balance with other factors. Thus the condition for the balance between non-adaptive and adaptive differentiation of island populations which permits the sort of trial and error process referred to above is that in which the effective amount of exchange between islands is of the order of the reciprocal of the effective size of population on them.

I would like to quote in full the abstract of my first paper on the subject since some statements in this paper taken from their context are probably the source of the misunderstanding. I have underlined [italized here] certain words here to emphasize qualifications that seem to have been overlooked.

*Evolution in a mendelian population ([Wright 1929]).*¹⁰⁴

“The frequency of a given gene in a population is affected by mutation, selection, migration and chance variation. The pressure exerted by these factors (excluding chance) and the points of equilibrium between opposing pressures are easily found. Gene frequency fluctuates about this equilibrium in a distribution curve, determined by size of population and the various pressures. [32|33] The mean and variability of characters, correlation between relatives, and the evolution of the population depend on these distributions. In too small a population there is nearly complete random fixation, little variation, little effect of selection, and thus a static condition modified occasionally by chance fixation of new mutations, leading to degeneration and extinction. In too large a *freely interbreeding population*, there is great variability, but such a close approach of all gene frequencies to equilibrium that there is no evolution under *static*

104. Wright's work is discussed in Provine (1971; 1978; 1986).

conditions. (Changed conditions cause a usually slight and reversible shift of the gene frequencies to new equilibrium points). With intermediate size of population, there is continual random shifting of gene frequencies and consequent alteration of all selection coefficients, leading to relatively rapid, indefinitely continuing, irreversible, and largely fortuitous, but not degenerative changes even under static conditions. The absolute rate, however, is *slow* being limited by mutation pressure. Finally in a *large but subdivided* population there is continually shifting differentiation among the local races, even under uniform static conditions, which, through intergroup selection, brings about indefinitely continuing, irreversible, adaptive and much more rapid evolution of the species as a whole."

The paper of which this was an abstract appeared in Genetics [Wright 1931]. It is noted there (p. 150) "In reaching the tentative conclusion that the situation is most favorable for evolution in a population of a certain intermediate size, one important consideration has been omitted. This is the tendency toward subdivision into more or less completely isolated subgroups in widely distributed populations". This is followed by mathematical reasons for the conclusion that with a certain degree of partial isolation of local races in an indefinitely large population "the rate of evolution should be much greater than in the previous cases".

There has been considerable development of the theory in later papers, especially with respect to the effects of nonadditive factor interactions and [33|34] multiple alleles. The conclusions as far as given in the 1929 abstract have however been modified only with respect to the sentence put in parentheses above. This sentence was based on too restricted a mathematical model and undoubtedly gives a wrong impression of the theoretical and actual importance of secular changes in the environment in causing evolutionary changes and ones that are practically irreversible with respect to genotypes. What I consider a sounder view in this respect was taken in a paper given before the 6th International Congress of Genetics in 1931 ([Wright 1932]). The possibilities for evolution in 6 cases were presented graphically in 6 diagrams which Dobzhansky has reprinted as fig. 23 (p. 340) of his book (2nd edition) [Dobzhansky 1941]. The cases in which an indefinitely large species is subject to qualitative change of environment (C) or is subdivided into partially isolated local races (F) are stressed as enormously more favorable for evolution than the case of a random breeding population of intermediate size (E) even though this is more favorable than either a very small population (D) or an indefinitely large one under the highly improbable condition of complete panmixia and no change of

conditions of selection (or an increase (B) or reduction (A) in the severity of selection not associated with any change in direction of selection.)

In recent papers ([Wright 1943a and 1943b]) I have shown that even with complete continuity of interbreeding but a limited rate of dispersal (or better a limited number of potential mates of any individual) there may be sufficient isolation by distance to make possible continual evolution even under uniform and unchanging conditions. Of course differences in conditions of selection in different regions and secular changes in direction of selection may (if properly balanced with other factors) make possible still more rapid evolution.

The conditions among horses during the tertiary as presented by W. D. Mathew [*sic*] ([Matthew 1926]) would seem highly favorable from the viewpoint of the mathematical theory for rapid evolution. The theory [34|35] is in fact in complete agreement with the conception of the evolution of horses expressed by Mathew [*sic*] in this paper as I noted in my 1932 paper referred to above [Wright 1932]. Conditions would also seem favorable in the case of elephants, camels and probably also ichthyosaurs. Conditions were certainly not favorable in the case of Rhynchocephalia as stated by Dr. Colbert.

Sincerely yours,
Sewall Wright

[end of *Bulletin 2*]

BULLETIN NO. 3

SEPTEMBER 25, 1944

The discussions of the Committee continue with this bulletin. Enough additional letters have been received to permit the publication of the next issue within a month's time. Considerable interest in the bulletins has been shown by several institutions and persons who are not members of the Committee. It will therefore become necessary to prepare an enlarged mailing list. The members of the committee are requested to send to Dr. Mayr a list of persons and institutions who should, in their opinion, be added to the mailing list.

As heretofore, a copy of all letters should be mailed to Dr. Mayr. It would facilitate the copying of the letters if the clean, original copy were sent to Dr. Mayr and the carbon copy to the respective correspondent.

The Steering Committee

The contents of this bulletin are as follows:

1. Evolutionary factors and the fossil evidence. Stebbins to Colbert, p. 1.
2. The origin of the genus *Pinus*. Babcock to Mason, p. 5.
3. Relative frequency of visible as compared to lethal mutations in *Drosophila*. Stebbins to Dobzhansky, p. 11—Dobzhansky to Stebbins, p. 12.
4. Comparative mutation rates in *Drosophila* species. Spencer, p. 16.
5. On the occurrence of sympatric speciation. Dobzhansky to Stern, p. 23.

[cover page |1]

June 8, 1944

Dear Dr. Colbert:¹⁰⁵

I read with great interest the mimeographed copy of your letter of March 20th to Dr. Mayr. The information contained in it shows clearly that the statement which I made in my letter to Dr. Dobzhansky of May 1st (pp. 18–19 of the bulletin [no. 1]), that "... the alternation between geologically stable and rapidly changing environments, ... has caused alternations between periods of explosive evolutionary activity and periods of

105. Original letter is located in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1." This letter is reproduced in its entirety here with the exception of a postscript asking Colbert to deliver a copy of this letter (copy enclosed) to Mayr. Colbert's acknowledgement (16 June 1944, in same folder) promises a detailed reply. If Colbert replied, it was not carried in the *Bulletin*.

relatively slow evolution or even stagnation,”¹⁰⁶ is not entirely supported by the fossil evidence, and is probably a naïve oversimplification. I believe, however, that it tells part of the story, at least in the case of plant evolution, and that it can be further supplemented.

Your emphasis on differential rates of evolution shows a most encouraging agreement with the evidence from plants. It strengthens my belief that instead of looking for unknown causes of evolution we should now focus our attention on the relative effect, whether accelerating or retarding, of the various known forces and factors, both external and internal, which have influenced the process. It seems to me that a paleontologist, when presented with a list of these forms as conceived by the geneticist and with the types of data on populations of living species which give evidence of their activity, could supply further evidence from fossil remains of past populations to give at least a partial estimate of their importance in evolutionary history.

As I understand them, the four principal forces affecting the rate of evolution are the two external ones of a) natural selection and b) the effects of sampling or random fixation, and the two internal ones of c) mutation rate (using “mutation” in its broadest sense, to include gross chromosomal as well as genic alterations) and d) degree of recombination or heterozygosity. The two first were discussed in your letter, although in my opinion not adequately in either case. For example, in mammals like the carnivores, isn’t [1|2] the biotic environment as important or more so than the secular one? If that is true, can you say that two different groups of mammals, even though they inhabit the same region, live under the same environmental conditions? I should not say, for instance that a bobcat and a mountain lion, both inhabiting the same mountain range, were living under the same conditions. Fluctuations in the number or alterations in the life habits of deer and other ruminants would have a great effect on the life and abundance of mountain lions, but relatively little on bobcats, while the latter would conversely be much affected by changes in the number or character of the smaller animals. On the basis of the hypothesis which I suggested on page 19 of the bulletin [no. 1], the relatively rapid rate of evolution of the felids might be explained by a sudden increase in numbers and diversity at the beginning of the Oligocene of certain animals upon which the early felids were adapted for preying. I realize that this type of evidence would be very hard for the paleontologist to supply, but feel that it must be taken into account before the effect of environmental factors can be dismissed in respect to a particular line of evolution.

In regard to the second force, random fixation, which has become understood chiefly through the work of Sewall Wright, population size

106. Ellipses are in the original document.

is, as Dr. Mayr says in his letter, an important factor. It is not, however, as Dr. Mayr implies, the only one. Perhaps Dr. Wright will write on this point himself, but as I understand his formulae they show that rapid evolution depends not on continued smallness of the effective breeding population, but on alternations between inbreeding and cross-breeding. Such alternations could be produced in a relatively large interbreeding population if it were subdivided into partially isolated smaller ones. In terms of animal distribution this would mean that even if a species were common, it would have the type of alternation required if its breeding communities were localized geographically, or if it practised [*sic*] some form of selective mating, whereby mating would usually be between males and females of the same interrelated community, but occasionally [2|3] or rarely between members of distinct and totally unrelated communities. I imagine that the application of this criterion to such extinct groups as the ichthyosaurs would be difficult or impossible, but in the case of groups with modern representatives this might be easier. For instance, how permanent is the organization of an elephant herd? If it extended over several generations, this might provide the necessary amount of inbreeding even though the population density were high. Another type of population change which would produce the necessary alternation between in- and cross-breeding would be great fluctuations in population size. Is there any evidence, for instance, that ichthyosaurs were very abundant at certain times and relatively scarce at others? This could, of course, result from fluctuations in the extent of the relatively shallow continental seas which I understand they largely inhabited. Such questions as these would have to be answered before Wright's formulae could be dismissed as inapplicable to a given instance of evolutionary progress. The stagnation of evolution in rare groups is not in the least evidence against Wright. If the group were broken up into small, permanently isolated breeding communities it would evolve rapidly for a very short time, to the extent of producing distinct races, subspecies, or perhaps species, but then, with all of its genes fixed, would become stagnant. Such has apparently been the fate of many rare plant species belonging to old groups, of which the giant Sequoia, *Sequoiadendron giganteum* [*sic: giganteum*], is perhaps the best known example.

The mutation rate, which I gather from your last paragraph on page 27, you consider as probably the most important force in determining rates of evolution of phylogenetic lines, is hard to estimate even in well known living animals like *Drosophila*, and at the present state of our knowledge no type of fossil evidence of which I can conceive would enable us even to guess at the importance of this force in phylogenetic lines, except by process of elimination.

The fourth force, the effect of recombination of genes due to genetic heterozygosity, is of course not an independent one, since it is

the resultant [3|4] of the amount of cross-breeding, of the mutation rate, and to a lesser extent the amount of genic elimination by natural selection. Nevertheless, it may be the most important of all in its immediate effect on the rate of evolution; since adaptation to a new environment or the development of a new way of exploiting an old environment depends in every case on the acquisition of a new *combination* of genetic characteristics, rather than the appearance and establishment of a single new character. In plants, the widespread, aggressive and weedy species are usually highly heterozygous, or possess mechanisms by which extreme heterozygosity may be brought every few generations. This heterozygosity is manifest not only through variability in the progeny of a single individual, but also through genetic variability between individuals of the same population, which can be demonstrated by growing them in a neutral garden. In such species, variability between different populations is also likely to be high. On the other hand, rare or local species, usually old ones show much greater uniformity in all of these respects, and give evidence of much greater homozygosity.

Now, would it be possible for the paleontologist to demonstrate that just before or during the beginning of a period of rapid evolution in a phylogenetic line, the group showed unusual variability, both between different individuals found in the same horizon and locality, and in those of the same geological age in different localities? It would be of particular significance if the variability were in characters which later became of adaptive importance in the mode of life adopted by the succeeding members of the line, i.e., in "preadaptive" characters. The variable condition of the teeth in Oligocene Equidae (*cf.* [Stirton 1940]) seems to be evidence of this nature. In the case of the carnivores which you discuss, is there any evidence that during the late Eocene or early Oligocene the felids or their immediate ancestors showed more variability at one particular horizon than the canids or viverrids? Unusual variability among individuals in the [4|5] same deposit would be of particular significance. I believe that this type of population analysis of fossil species on a comparative basis would be of greater value to the geneticist as a means of relating his fund of information to that of the paleontologist than any other facts which the latter could supply.

Yours very truly,
G. Ledyard Stebbins, Jr.

July 31, 1944

Dear Dr. Mason:

Recently I had an unexpected opportunity to examine the present geographic distribution of the genus *Pinus* in relation to such phyloge-

netic arrangements of the sections as Shaw's, Beissner's and Pilger's. The result of this superficial examination was a strong impression that the region of origin of the genus must have been in Asia or north of the present continent of Asia. Recalling your verbally expressed opinion that the pines probably originated in North America, I decided to look into the matter, somewhat more carefully. So I made a preliminary review of the fossil evidence and have examined some of the other literature having a bearing on the subject. I am sending you this brief summary of my findings in the hope that you may consider it worth while to go into the subject very thoroughly yourself. Meanwhile, I should be grateful for your reaction to my tentative conclusion.

1. *Present distribution of species and section* (from Pilger).- Of the 77 species included in Pilger's treatment ([Pilger 1926]) 28 species or 40% are of the Old World and 49 or 60% are in North America. This might seem to indicate that America was the region of origin. But such an inference does not agree with the distribution of the sections in the two hemispheres, which is as follows:

Old World:	1,	2,	3,	<u>4</u> ,	5,	6,	<u>7</u> ,	<u>9</u> .
No. Amer.:	1,	2,	3,	5,	6,	<u>8</u> ,	<u>10</u> ,	<u>11</u> .

Section 1-3 are the most primitive and they, as well as Sections 5 & 6, occur [5|6] in both hemispheres. Sections 4, 7 and 9 are in the Old World, while 8, 10 and 11 are exclusively North American. To my mind this suggests very definitely one center of origin for the two continents, located in a nearly intermediate position. What is more reasonable than to assume this location to have been in Alaska or Kamtchatka [*sic*: Kamchatka], or the arctic continent to the north of that region?

2. *Evidence from Florin's recent review* ([Florin 1940]) *of the fossil conifers of southern lands*. Although this very thorough study is concerned with the Southern Hemisphere, the author reaches two conclusions which are of significance for the present discussion. (1) He recognizes (p. 88) two regions of early differentiation for the conifers of the world, the northern Arcto-Carboniferous and the southern Antarcto-Carboniferous, and states that as early as late Paleozoic "the conifers of the Northern Hemisphere were far more richly developed and widely distributed than those of the Southern." (2) In summarizing his discussion of the unique genus, *Libocedrus* (p. 91) which "differs from all other living genera, in that it is well represented in the recent coniferous vegetation of both the north and south temperate zones", he states: "*Libocedrus* may therefore have originated in the north, and then spread not only east and west but also south to New Zealand and southern South America." Thus, for a genus belonging in a family close to the Pinaceae, Florin assumes a center of origin very similar to the one suggested above for *Pinus*.

3. *The fossil evidence for Pinus.*- (a) The most ancient fossil records for *Pinus* known to me are Heer's reports [Heer 1868–1883: vol. 5] of *P. Nordenskiöldi* from Jurassic deposits in northern Siberia (at two stations in the northern Lena R. valley at about 71° N. lat.) and in northern Norway (Andö I., about 69° N. lat.). Two other species occur at both the Lena R. and Andö I. stations. The two genera represented by these species, *Phoenocopsis* and *Baiera*, are recognized by Seward as Jurassic or even older. Furthermore, Seward ([1941], pp. 374, 376) tabulates these fossils of Heer as Jurassic; [6]7 but he does not mention *Pinus Nordenskiöldi* anywhere in his book. It is possible that a search of the literature on other Jurassic plant fossils listed by Seward (1.c.) [1941] would bring to light other pine species of as great [an] age as *P. Nordenskiöldi*. In vol. 4 of the same work Heer reports this fossil pine from Jurassic deposits in southeastern Siberia (Ust.-Balei, Upper Amur and Bureja) and these are tabulated by Seward (1.c.) [1941] as Jurassic. And in vol. 3 he reports it from a Tertiary formation in Spitzbergen. Possibly this would now be recognized as Cretaceous as is the case in some of Heer's other supposed Tertiary fossils (Seward [1941], p. 402). In discussing the latter specimens, Heer points out that the seeds are wingless and assumes that the wings have fallen off. But it seems just as likely that the seeds were actually wingless. In all three phylogenetic classifications of present-day pines the most primitive section contains the species with wingless seeds. At any rate, it seems fairly certain that at least one species of pine existed in the Jurassic period and was even then spread from eastern Siberia across arctic Eurasia to Norway.

(b) During the Cretaceous period *Pinus* species certainly existed in western Europe and in eastern North America. Concerning western Europe, see Pilger ([1926]) on fossil pines and Seward's discussion of Cretaceous conifers. On eastern North America I have consulted Hollick and Jeffrey's paper ([1909]). I believe Cretaceous pines have also been reported from Greenland. The fact that Jeffrey named one of his New York fossils *Prepinus* is, I think, no more significant than the fact that fossil forms which are apparently intermediate between *Pinus* and *Cedrus* have long been known from Cretaceous deposits in western Europe. On the contrary, the very fact that such less differentiated forms existed both in western Europe and eastern North America during the Cretaceous period would seem to indicate a center of origin in Asiatic Arctica. This is certainly indicated by the Jurassic *P. Nordenskiöldi*.

4. *Comparison of Pinus and Cedrus.* Although *Cedrus* is now restricted to four species, which are endemic respectively in the Himalayas, Asia Minor, [7]8 Cyprus, and the Grand Atlas, the fossil evidence points to a northern Asiatic center of origin. According to Pilger ([1926]) *Cedrus* fossils have been reported from Cretaceous deposits in western Europe and from Tertiary remains in France and

Germany as well as from eastern Siberia. The last mentioned locality, from the original report (Heer [1868–1883], vol. 5) is actually in south central Siberia about 100 km. west of Krassnojarsk [*sic*: Krasnoyarsk]. There in a Miocene deposit were found cone scales, seeds and leaves of a species which, according to Heer, is undoubtedly close to the present-day Himalayan species. Furthermore, well preserved specimens of *Cedrus* wood have been discovered in Tertiary auriferous gravels in California [Barghoorn and Bailey 1938]. The wood of these specimens, being neither mineralized, lignitized nor carbonized, can be distinguished from that of existing species of *Cedrus* by the absence of ray tracheids; and a similar difference exists between certain fossil pines and existing species. Although it must be admitted that the oldest known fossils of *Cedrus* are from western Europe, yet similar or older records may eventually be discovered in Asia. It is certain that during Tertiary [times] the genus was distributed in Europe, Asia and western North America, from which it may be inferred that Asia or adjacent Arctica is the probable region of origin. This is in line with the general conclusion of Seward ([1941], pp. 387, 400) that the origin of the conifers of the Northern Hemisphere was in the arctic region. From the known fossil records of *Cedrus* and *Pinus* the two would appear to have had a common region of origin in Asiatic rather than American Arctica.

5. *Discovery of a relic pine in the Grand Atlas.*— In view of the existence of a relic cedar in the Grand Atlas Mts., it might seem strange that no relic pines have been reported from that region. In 1927 Maire and Peyerimhoff [*sic*: Peyerimhoff] [1927: 1515–16] reported a relic variety of the Laricio pine as *P. nigra* var. *mauretanica*. This name was changed in 1941 [Emberger and Maire 1941, 4: 920] to *Pinus pyrenaica* ssp. *mauretanica*.

6. *Anatomical evidence agrees with or partially supports the phylogenetic [8|9*] classification of the pines based mostly on external morphology.*— (a) Two Japanese, K. Doi and K. Moriwaka [1929] made an exhaustive study of leaf anatomy in *Pinus* and found general agreement between their own classification, worked out on that basis, and Pilger's [1926] classification. (b) Bailey's study of wood anatomy and its bearing on the evolution of the pines [probably Bailey and Kerr 1935] also supports the recognition (by Pilger and others) of the hard pines as farther advanced in evolution than the soft and nut pines. However, Bailey (p. 293) says that the type of hard pines represented by *P. resinosa* in North America and *P. silvestris* in Europe represent the most highly developed and specialized condition (anatomically) among living pines. Since these two species are placed in Section 5 by Pilger, i.e., midway instead of near the advanced end of the series, there is not complete correlation of the evidence from anatomy and external morphology.

7. *Significance of high specific differentiation in western United States and Mexico.*- The mere fact that over one-fourth of all the species of pines recognized by Pilger (his Sections 10 and 11) are endemic in western U.S. or Mexico might suggest that this region was the center of origin of the genus. But I believe that the evidence presented above shows the strong probability that the genus originated in northern Asia or Asiatic Arctica. If this inference is correct, our western and Mexican hardwood and closed-cone pines must have become differentiated from more primitive forms in comparatively recent geological time-Tertiary-Quaternary. The known existence of *Prepinus* in northeast North America, and of such primitive species as *Pinus albicaulis* and *P. strobus* in eastern U.S., and *P. flexilis*, *Lambertiana monticola*¹⁰⁷ and *ayacahuite* in western U.S. or Mexico, together with the morphological evidence on interconnecting species in intermediate sections (*cf.* Shaw), certainly warrants the assumption that the twenty species in Pilger's sections 10 and 11 became differentiated from more primitive ancestors in the regions where they now exist. It is also reasonable (in view of the chromosomal [9][10] uniformity in *Pinus*) to assume that this process of differentiation was made possible by gene mutations and natural selection under the influence of the extreme environmental changes which occurred throughout these regions during Tertiary-Quaternary.

8. *Significance of the evidence on Pinus for the evolution of higher plants.*- If the evidence I have presented is to be taken seriously and if my interpretations are correct, then the general evolutionary picture in *Pinus* has a definite bearing on the general question first suggested by Dobzhansky [(J)Bull. no. 1, pp. 1-3) as to the amount of evolution that has actually been going on, especially in arboreal plants, during the Tertiary and Quaternary periods. According to Seward [1941, p. 396] the deposits in which *Prepinus* and certain pines were found are Upper Cretaceous. If this is correct, then there has been a great deal of evolution and speciation in *Pinus* during Tertiary-Quaternary.

In conclusion I will merely state that I became interested in *Pinus* when I was struck by the general similarity between it's [*sic*: its] present-day distribution and that of *Crepis*. Another point of similarity seems to be in the location of the region of highest speciation with reference to the center of origin. In *Crepis* it is the Mediterranean region which is far removed from north central Asia, the center of origin. In *Pinus*, it is Mexico and western U.S., which is also far removed from arctic Asia. It is my earnest hope that this little effort on my part will be of some help to you in the thorough review which I trust you will make of all the available fossil evidence on *Pinus* and its relatives and the critical interpretation which you will make of that evidence.

Sincerely yours,
E.B. Babcock [10][11]

107. The original reads "*Lambertiana, monticola*."

[July 28, 1944]¹⁰⁸

Dear Dobzhansky:

The question has recently come up in one of my classes of the relative frequency of visible as compared to lethal mutations in different species of *Drosophila*. Dubinin's work in *D. melanogaster* seems to indicate a higher frequency of visibles in relation to lethals than does yours on *D. pseudoobscura*. Is it your impression that this represents an actual difference between the two species? One of my students suggested that the greater abundance of inversions in *D. pseudoobscura* would tend to preserve more mutations in the heterozygous condition, and therefore given the same mutation rate of lethals and semi-lethals, the number of these mutations existing in natural populations would be greater in *D. pseudoobscura* than in *D. melanogaster*. On this basis the same rate should also give a greater expectation of visible mutations in *D. pseudoobscura*, so that if these are actually less, the mutation rate for visibles must be much lower in that species than in *D. melanogaster*. This supposition seems to agree well with the report of Spencer for October, 1943, to the Committee on Genetics and Paleontology, (see below [in *Bulletin* 3]),¹⁰⁹ which states that the visible mutation rate in *D. melanogaster* is higher than that of the three other species studied by him. Yet on page 58 of your book you state that in *D. pseudoobscura*, "Mutant genes producing visible external effects are likewise common." Does this mean that in some populations visible mutations are in as high concentrations as those reported by Dubinin's group for *D. melanogaster*? The significance of all this to me lies in the possible correlation between the high visible mutation rate of *D. melanogaster* and the spread of this species as a "weed" or "pest" in new habitats associated with man. Couldn't this be an instance of evolutionary opportunism caused at least in part by a preadaptive high mutation rate?

Another question which has come up is the relative effect on the mutation rate under natural conditions of external conditions as compared to alterations in the genetic background.¹¹⁰ There seems to be every reason to believe that the dosage of radiations, temperature shocks, chemicals, etc., which are [11|12] required to induce mutations are so drastic that they would rarely be encountered in nature. On the other hand, instances seem to be accumulating of individual genes or gene complexes which affect the mutation rate of one or more other genes. I should therefore like to have your opinion of the possible validity of the hypothesis that in nature rates of evolution are more often affected by changes in the genetic background than by external

108. No date is provided in the mimeographed *Bulletin*. Cain's dating derives from Stebbin's reply of 18 August 1944 elsewhere in this *Bulletin*.

109. Cain's intervention is in [] brackets. Mayr's intervention is in () brackets.

110. This sentence is not clear in the original.

influences. If this hypothesis could be established as a generalization with any degree of truth in it, its implications for the dynamics of evolution would be very great.

Yours very sincerely,
G. Ledyard Stebbins, Jr.

August 18, 1944

Dear Dr. Stebbins:

I wish I could give satisfactory answers to the questions which you raise in your letter of July 28th. Unfortunately, reliable data on comparative mutability in different species of *Drosophila* (or of any other genus for that matter) are very scanty.

First of all, let us distinguish clearly the three problems the independence of which may not be quite obvious to non-geneticists. First, we may compare the accumulated stores of mutants carried in natural populations and expressed in the phenotype, thus causing the observable variability and polymorphism. Second, we may examine the accumulated stores of recessive mutants carried partly or wholly in a concealed condition owing to their individually low frequencies, causing most of them to be present only as heterozygotes. Third, we may make qualitative and quantitative comparisons of the mutation processes themselves, that is of the mutants as they arise *de novo*. It is obvious that the stores of mutants, both concealed and expressed in the phenotype, are constantly being replenished through the mutation process. Nevertheless, the mutants that are preserved and accumulated in the populations are, for several reasons which need not be discussed in this letter, by no means [12|13] random samples of the mutants which arise *de novo* in each generation. It would not be too surprising [*sic*] to find that the mutation rates in some species that show a high phenotypically perceptible variability are actually smaller than in some species which seem externally uniform to a systematist. It may well happen that some groups which undergo rapid evolutionary changes have smaller mutations rates than groups which are static in [a] paleontological sense. After all, species of *Drosophila* are now classical examples of mutability, and yet with the exception of some tropical species (*D. cardini*, *D. polymorpha*) they show on the whole less variability in externally visible characters in natural populations than do many other groups of insects. It would be very rash to infer that the mutation rates in *Drosophila* are lower than in most insects.

Comparing the natural populations of *D. melanogaster* and *D. pseudoobscura* with respect to their phenotypically expressed variabilities, I hesitate to assert either that they are similar or that they are different. Dubinin and his collaborators have made efforts to find visible mutants in *D. melanogaster* populations, and have found great many such mutants. I have not attempted a census of visible mutants in

D. pseudoobscura, partly because I happen to be an exceptionally poor “mutation finder”, and know that I would overlook most of them. All I know is that some visibles do occur in *D. pseudoobscura*, as they do also in other species of *Drosophila* studied in this respect particularly by Spencer (who, by the way, is probably the best “mutation finder” among American geneticists). I think that reliable comparative data on the incidence of visible mutants in *Drosophila* species could be obtained only if they were collected by a single investigator, if then.

As to the concealed variability, only very few species of *Drosophila* have so far been examined in this respect, and the two relatively well known species are again *D. melanogaster* and *D. pseudoobscura*. This pair of species are, in a way, least suitable for the purpose of comparative studies on variability in natural populations. *D. melanogaster* is, in the Temperate Zone where [13|14] all the work has so far been done, an introduced “animal weed” which follows man very closely. In central Russia and in the northern United States it apparently does not survive winters outdoors, and its population is reduced in winter to a few foci in human dwellings. There is no wonder, then, that the data of Dubinin’s school on Russian populations, and those of P. T. Ives on American *D. melanogaster* do not agree very well. On the other hand, *D. pseudoobscura* is only seldom found in the scavenger role, and there is no evidence that it increased its distribution range through association with man. Comparisons of the frequencies of recessive mutant genes with visible external effects in different species meet, of course, with the same difficulties as do comparisons of the frequencies of the phenotypically expressed visible variants—a good “mutation finder” will find more of them than a poor one. All I can say is that a fair number of major mutants were brought to light by genetic analysis of the autosomes of the wild *D. pseudoobscura*. Of course, it remains possible that in *D. melanogaster* such mutants are more common. The frequencies of recessive lethals can be estimated reasonably accurately, since here the “personal equation” can, despite some technical difficulties, be overcome. The data available show that concentrations of lethals vary quite appreciably in different populations of the same species. Thus, Mexican populations of *D. pseudoobscura* have twice as many lethals in the third chromosome as do California populations, and this difference is almost certainly due to the breeding structures of these populations and not to mutation rates. The concentrations of lethals found in *D. melanogaster* by Dubinin’s school in Russia and by P. T. Ives in the United States are also different, but not necessarily higher than in *D. pseudoobscura*.

Now, the results of studies on the mutation process itself are no more conclusive. It so happens that in *D. melanogaster* we have abundant data on mutation rates in the X-chromosome, while the best known chromosome in *D. pseudoobscura* is an autosome! It does seem that *D. melanogaster* is more [14|15] mutable than *D. pseudoobscura*, but

I do not regard the available data [*sic*: data] conclusive. Perhaps the most reliable data, aside from those of Spencer which you refer to, are by Timofeeff-Ressovsky [1936] on mutabilities of *D. melanogaster* and *D. funebris*. These data show that *D. melanogaster* produces relatively more sharp mutants modifying the coloration of the eyes and of the body, while in *D. funebris* weakly penetrant mutants, particularly those affecting wing venation, are more abundant.

I am very much in sympathy with your opinion that in natural populations the genetic controls of the mutability are more important than external conditions, but here again we must admit that our knowledge is quite insufficient. According to Timofeeff-Ressovsky, the temperature coefficient of the mutation process in *Drosophila* is fairly high, but the problem is complicated by the lack of decisive information regarding the proportionality of mutation to time or to the number of cell generations.¹¹¹ Not enough is known regarding the effects of temperature variations within the ecological range on the mutation frequencies, the data of Zuitin on this subject being far from convincing. We must admit, I think, that when a species of *Drosophila* is distributed over a wide range of climates, the populations which live in warm climates are likely to produce more mutations per unit time than populations in cold climates. Nothing is known, however, about which temperature is the effective one: the annual mean, or the mean for the breeding season only, or the temperature maxima that are encountered? Further studies on genetic controls of mutability are urgently needed, but it is safe to say that these controls are very effective in evolution.

The problems which you raised in your letter are evidently of prime importance for understanding, not to speak of the control, of the process of evolution. The fact that next to no investigations bearing on these problems have been made, and that only relatively few geneticists are even aware of [15|16] these problems, may seem discouraging. But the same fact may be a source of optimism: it suggests that the most fundamental discoveries in genetics are yet to be made, and the most far-reaching theories yet to be constructed!

Sincerely yours,
Th. Dobzhansky

*Comparative Mutation Rates in Drosophila Species*¹¹²

By Warren Spencer

Among biologists in general and geneticists in particular, mutation, the sudden origin of a discontinuous change arising in an individual and

111. Timofeeff-Ressovsky (1937) provides elaboration.

112. A footnote placed in the original *Bulletin* here reads: "Presented at the July 1943 New York meeting of the Committee."

capable of transmission to the offspring of that individual, is recognized as one of the important factors whose interplay has brought about and is continuing to bring about organic evolution. Geneticists are likely to think of mutation as the keystone in the evolutionary arch. It would perhaps be nearer the truth to recognize all the interacting factors as necessary, but varying in relative importance in time and space.

Whatever the eventual role assigned to mutation as a factor in evolution, at present it would seem profitable to raise some questions concerning the origin, distribution, and survival of mutations in individuals, populations, and species.

The genus *Drosophila* offers unusual opportunities for a study of some of these questions. Thru [*sic*] the pioneering work of Morgan, Bridges, Muller, and Sturtevant and their colleagues on *Drosophila melanogaster* many hundreds of mutations have been found and their positions in the chromosomes accurately mapped. The epochal discovery by Muller of artificial transmutation by X-rays made possible a stepping up of mutation rate to a point where many hitherto insoluble problems concerning mutation could be successfully worked out. Then came the recognition of the significance of the salivary chromosome pattern as a constant chromatin architecture by Painter and Stone. Furthermore the [16|17] genus is rich in species (seventy-five new species and subspecies of North American *Drosophila* have been described by Patterson and colleagues in the past two years). It seems likely on the basis of past collections and species already described that there are more than a thousand extant species in this genus. Already upwards of forty cases of hybridization between species and subspecies have been studied and the surface has barely been scratched.

Much of my own work over the past twenty years has dealt either directly or indirectly with the study of natural mutations in *Drosophila*. (We have had in culture at various times some sixty different *Drosophila* species and have observed several hundred natural mutations, mostly in the species *hydei*, *funnebris*, *melanogaster*, *immigrans*, and *robusta*. I make no apologies for giving some general impressions on visible natural mutations. I shall raise some questions, answer none of them in any but tentative fashion and leave others entirely unanswered. However, it would seem that the chief value of such a meeting as this is to consider together problems and their possible solutions.

The first question I would raise is: "Do the various species of the genus *Drosophila* have observably different rates of visible mutation?" We should keep in mind that Demerec, Neel, Tiniakov, and perhaps others in studying *D. melanogaster* and Mampell in studying *D. persimilis* have discovered rapidly mutating stocks, containing apparently "mutator" genes. It becomes evident then that a single experiment, however extensive, but utilizing one stock from each species might not give a valid answer, particularly if mutator genes of varying degrees of activity

are, as seems probable, not uncommon in *Drosophila*. Thus an impression gained over a period of years and formed from many diverse stocks might after all give a truer answer than a single elaborate and accurately recorded experiment. My impression from the finding of several hundred natural visible mutations is that *D. melanogaster* has a higher mutation rate per individual than does *D. hydei*, *D. robusta*, *D. immigrans*, or *D. funebris*. [17|18] This is based on the autosomal recessives discovered, though here the evidence is indirect as a mutation may have arisen many generations before its discovery. However, the much more critical evidence from sex-linked mutants indicates the same thing. Thus in *D. melanogaster* 12 sex-linked visibles at 10 loci were observed, while in looking over at least 10 times as many *D. hydei* only 16 visibles in 13 loci were found (excepting the special case of bobbed to be discussed later). These data indicate a sex-linked visible mutation rate in *melanogaster* about 7 times as high as in *hydei*. I would not claim any exactness for this figure, but I am pretty well convinced that *hydei* mutates on the average less frequently per individual fly than does *melanogaster*. I have the same impression of *funebris*, *robusta*, and *immigrans* as mutating less rapidly than *melanogaster*. The genus *Drosophila* has been divided into several subgenera by Sturtevant. Of these the two largest subgenera in number of species are *Sophophora* and *Drosophila*. To the former belong a number of species which have served for genetic studies, namely *melanogaster*, *simulans*, *ananassae*, *pseudoobscura*, *willistoni*, *affinis*. In the subgenus *Drosophila* the species *virilis*, *hydei*, *funebris*, *immigrans* and *robusta* have been most extensively studied genetically. Sturtevant informs me that he considers that *simulans* mutates as readily as does *melanogaster*. In general I would gather from the records of mutation in the *Sophophora* subgenus that they mutate more frequently than do the species in the *Drosophila* subgenus[.] (I would like to ask Dr. Demerec who has had considerable experience with *virilis* and *melanogaster* what his impression of relative mutation rate is?)

The second question I would raise is this. "Can the mutation rate in individual homologous loci vary from species to species and independently of the general mutation rate?" To consider this question it must first be reasonably established that homologous loci exist in the different species and that at least in many cases these can be recognized. The ideal test of homologous or parallel loci is by direct crosses and study of hybrids for [18|19] evidence of allelism in what appear to be identical or similar mutants. Unfortunately this has not been possible in most species investigated genetically. However, Sturtevant was able in crosses of *melanogaster* and *simulans* to show that a large series of mutant loci were actually homologous in the two species. Of further interest is the fact that he was able to predict many cases of allelism before the crossing test was made. If, as seems likely, blocks of chromatin have re-

mained intact from species to species in the evolution of the genus, linkage relations should be added [as] indirect evidence of homology in some cases. Thus there is a considerable series of sex-linked mutants which appear to have occurred over and over again in several *Drosophila* species investigated. Some of these are white eye, vermilion eye, miniature and dusky wings, yellow body, scute bristles, forked and singed bristles, and bobbed bristles. In addition to these being sex-linked and similar in phenotypic effect, there are additional points of evidence such as the close linkage of miniature and dusky, the fact that only one locus has ever been found in any *Drosophila* species which gave white eyed mutants or yellow bodied mutants, etc. When it comes to homologizing autosomal loci one must proceed with considerable caution. While the occurrence of reciprocal translocations of sections of chromosome arms seems to have been a very rare event in *Drosophila* speciation, Wharton has recently added much cytological evidence for the occurrence of fusion of chromosome arms and paracentric inversions. Such events properly seriated could result and perhaps have resulted in much autosomal scrambling of the chromatin pattern. Thus it may be questioned as to whether one will find whole autosome arms which have remained intact from species to species. That is not to say that instances of this sort may not be found repeatedly in species groups. My own position on the establishing of autosomal homology was at one time that the evidence would be very strong if a polymorphic mutation with many phenotypic effects were to be found in two species and that these could be considered as homologous, particularly if the mutant were of a relatively rare type. [19|20|?]

However, I am led to a conservative position by experience. In two cases which seemed almost ideal, irregular and grooveless in *D. hydei*, loci in the fifth and sixth chromosomes respectively, mutants apparently identical in their multiple phenotypic effects have later been found in the fourth chromosome. In spite of this there seems good reason to believe that further study will make possible the establishing of many autosomal homologies. Thus the dot-like chromosome present in most *Drosophila* species has given a mutation picture quite similar but less extensive than that of the X-chromosome. One can mention grooveless, bent, Gap and Minute-4 as examples of apparent parallels in this tiny block of chromatin.

A survey of the mutants in the different *Drosophila* species indicates that there are specific loci in certain species that mutate much more frequently than would be expected on the basis of the general mutation rate for that species and the mutation rate for apparent parallel loci in other species.

Bobbed, a sex-linked and sex-limited bristle mutant which is clearly a parallel or homologous locus in many *Drosophila* species is a case of this sort. In *Drosophila hydei* wild populations carry a large series of

bobbed alleles ranging from extreme types at one end which are not only lethal in homozygous form but lethal in combination with moderate bobbed alleles to types at the other end of the series which in themselves have no phenotypic effect and can only be seriated and recognized as alleles of different strength by using strong bobbed alleles as sensitizers. While bobbed is known in other species in none of them has such a large allelic series been found.

In *Drosophila immigrans* an autosomal net-vein locus has given a large and indefinite series of alleles of different strengths. Many of these alleles, some of them partial dominants, have been demonstrated by the analysis of wild *immigrans* populations. Sturtevant first called the reader's attention to this case. While there are several net-like loci known in *D. melanogaster*, any one [20|21] of which might be homologous to net in *immigrans*, none of them show the high mutability of the net locus in *immigrans*.

The author has tested a number of wild strains of *D. transversa* for the presence of autosomal recessive mutants. He has repeatedly (four times) found a javelin-like mutant.

In *Drosophila melanogaster* trident is a case of a highly mutable locus though here modifying factors may play an important role in phenotypic expression. It seems likely that as other species of *Drosophila* are intensively investigated new cases of highly mutable loci will be found. These cases are not to be interpreted as of the same type as the mutable genes which Dr. Demerec has discovered in *D. virilis*. It seems well established that the *Drosophila* species differ in the picture of visible mutation at specific loci as well as in general mutation rate.

The third question I would raise is: "Is the phenotypic expression, particularly as regards penetrance and dominance relations the same in all *Drosophila* species?"

For over ten years the author made a parallel study of the mutation picture in *D. hydei* and *D. funebris*, with less extensive observations on certain other species. The author and Timofeeff[-]Ressovsky who also worked on the genetics of *Drosophila funebris* came to much the same conclusions concerning this species. Timofeeff [1936] summarizes the qualitative differences in the mutability of *funebris* as follows. Of 83 mutants in this species recorded by himself and the author only 21.7% showed 100% expression in homozygous stocks. In contrast, of 107 mutants found by the same workers in other *Drosophila* species 67.3% gave 100% expression in homozygous stocks. Of 502 mutants listed in *melanogaster* 17.2% are dominants. Of 94 mutants in *funebris* 41.5% are dominants. Body and eye color mutants constitute about 3% of the total in *funebris* and about 25% of the total in *melanogaster*. In contrast approximately 35% of the mutants in *funebris* affect the wing veins as against [21|22] 7% in *melanogaster*. H. A. Timofeeff-Ressovsky [1930] has reported a similar trend in X-ray induced mutants. Sturtevant con-

siders that the difference between the mutation picture in *funnebris* and other species is purely a quantitative one. This opinion is based on his own experience with the species. I should rather agree with Timofeeff that the difference is primarily a qualitative one with a generally lower mutation rate than in certain species of the subgenus *Sophophora*.

The final question which I should like to raise is this: "If there are differences in mutation rates as between different species within the genus *Drosophila*, and differences in relative mutation rate at certain loci in some species, and differences in the general phenotypic expression of mutants from species to species, have these facts any significance in the evolution of the group?"

If, as seems likely, the mutation rate in *Drosophila melanogaster* is higher than in species of the subgenus *Drosophila*, this fact does not seem to have resulted in a marked increase of closely related species and subspecies. It is true that most of the collecting of *Drosophila* has been done where *melanogaster* is apparently an introduced species, and in fact there is no clear evidence as to where it may have originated. It is extremely successful in establishing colonies associated with man from the tropics to latitudes north of the northern border of the U.S.. Patterson's [*sic*: Patterson's] collecting data give it as by far the most abundant species in numbers taken. However, his collections have been made largely in places where domestic or introduced populations might thrive. In any case *simulans* is the only closely related and hybridizing species yet discovered, and no variant forms which could be considered subspecies are known. This is in marked contrast to the *repleta* group with over thirty closely related species and subspecies, several cases of hybridizing forms, and the *virilis* group, where several very closely related species or subspecies have been found. It would appear that relatively high mutability alone [22|23] does not serve to promote rapid evolution at levels which result in speciation.

However, a moderate rate of mutation such as that found in any of the species of *Drosophila* investigated would seem to furnish ample building material for the erection of an evolutionary superstructure providing the necessary conditions of geographical and/or physiological or ecological isolation were operating.

It is hardly to be supposed that the mutants which the geneticist deals with are the most important one[s] for selective action either positive or negative, and yet some of them may be. The presence of what appear to be genetic loci with abnormally high mutation rate and capable of mutating to a large series of distinguishable alleles might perhaps be interpreted as having little significance. However, there is an alternative explanation. As gene action is now known to depend upon a delicately balanced interaction of factors coming into operation at different times, may it not be that these cases of high mutability represent a particular timing in gene action which makes possible a phenotypic

expression of that locus variability which ordinarily does not reach the level of phenotypic expression except in rare and extreme mutants. On this interpretation the species, probably any species, contains a vast reservoir of untapped genic variability awaiting the interplay of new environmental forces or the action of new genetic backgrounds for expression and possible selective action.

It would seem then that a valid experimental approach might be the testing of what appear to be identical races or populations for hidden variability and particularly for adaptive genetic complexes. However, such experimentation on a sufficiently large scale must await a more generous subsidy in men and money than is likely to develop in the near future.

[end of paper by Spencer]

August 19, 1944

Dear Dr. Stern¹¹³[:]

I would like to add some remarks to your discussion of the problem [23|24] of the origin of isolating mechanisms (in your letter to Dr. Mayr, No. 2 of this Bulletin).

We all agree that the process of speciation in obligatorily sexual and cross-fertilizing organisms usually takes place via geographic isolation and geographic race formation. Reproductive isolation follows, rather than precedes, genetic differentiation in space. The topic under discussion is, consequently, not whether sympatric speciation is the rule, but whether it occurs in exceptional circumstances or does not occur at all. So stated, the problem is very difficult to settle. We are not discussing any concrete group of organisms in which sympatric speciation has been observed to take place or inferred on [the] basis of tangible evidence; we are considering theoretical possibilities which might arise in hypothetical circumstances. And when I think about the incredible tricks played by some organisms (consider the utterly fantastic meiotic mechanisms discovered by Metz in *Sciara*), I am almost convinced that the tour de force of sympatric speciation must exist somewhere!

Let us try to define what we mean by sympatric speciation. It is development of reproductive isolation between populations the members of which normally occur in such a close spatial proximity that they frequently meet owing to active migration or to passive transport. The difficulty of such a process, which seems well-nigh insuperable, is that here the development of reproductive isolation must precede the accumulation of a multiplicity of genic differences, in other words that reproductive isolation must antedate the genetic divergence which makes

113. The original letter is located in Stern Papers, folder "Dobzhansky, Theodosius #3."

the populations really distinct. Of course, members of the same breeding units, even brothers and sisters, may differ in many genes. But the important think [*sic*: thing] is that the maintenance, not to speak of accumulation, of multiple gene differences between *populations* does require that the rate of convergence owing to interbreeding be less than [*sic*: than] the rate of divergence due to selection or other causes. The role of geographic isolation in speciation lies precisely in that it acts as an extrinsic factor which [24|25] reduces the rate of interbreeding of populations before this reduction is accomplished by intrinsic means—by reproductive isolation.

It is the quantitative aspect of the problem of isolation that seems to me really crucial for evaluation of the possibilities of sympatric speciation. It is not necessary to suppose that the genetic differences once present between populations would always be wiped out in a generation unless these populations are either geographically or reproductively isolated. But I find it difficult to imagine a set of conditions which are likely to occur in reality, and under which a stable equilibrium between the forces of convergence and divergence, not to speak of a steady divergence, would ensue without either geographic or reproductive isolation. In your letter you discuss the very plausible possibility of mating preferences being conditioned by occupation of different ecological niches. It is indeed conceivable that the same insect species may form colonies feeding on different species of trees in the same forest, and that the individuals grown on each species of tree would exhibit a preference for homogamic mating. In order not to have the situation become a special case of geographic isolation (the island isolation which you mentioned), we must assume our insect to be mobile enough, so that an individual is likely to encounter various trees and their inhabitants within its lifetime. Given such a system, I admit that the multiple genic differences between the populations of the different trees, *provided these differences are present at the outset*, need not be wiped out by interbreeding within a single or a few generations. But, *building up of such differences* would necessitate a condition that the fact of development on different species of trees would act on the respective insect populations as a selective agent so powerful that it would overbalance the gene convergence due to the occasional interbreeding. Alternatively, we must assume that the inhabitants of the different trees possess such intense preferences for homogamic matings that the sexual isolation so acquired permits relatively weak selection pressures to be operative. In [25|26] the absence of experimental or observational data we can only guess whether or not these contingencies are likely to be encountered at all.

Essentially similar considerations apply to the other interesting possibility which you discuss, namely that of a recessive mutant *a* which produces a homozygote *aa* reproductively isolated from both *AA* and

Aa. This seems to be a workable scheme, provided that the mutation brings in its train a reproductive isolation which is either complete or, at any rate, so strong that the occasional interbreeding of aa with AA and Aa does not outweigh the differentiating forces (selection, genetic drift, mutation) acting divergently on aa on one hand and on AA and Aa on the other. This might be the case if your two Hydractinias have spawning times which are very nearly or completely non-overlapping. But I submit that the probability of a sharp mutational change in the spawning time, which would prove to be adaptively useful, or even neutral, to the species, does not seem to me very great. Indeed, if there is an unoccupied ecological niche for a species with a spawning time different from the existing species, the transition from the existing to the new species is much more likely to be accomplished by building up suitable gene complexes from minor mutants (multiple genic causation), rather than by a single mutational saltation.

Among the evolutionary situations which excite my curiosity are those which seem to obtain in certain parasites, but unfortunately I do not know enough about the concrete cases to discuss the situations in anything but a superficial way. It may be interesting to consider populations of a single species of Mallophaga living on two sympatric species of birds. If the birds in question have different ecological preferences, the populations of their parasites may exchange individuals very rarely and eventually not at all. This may, then, be a case of a secular isolation distinct from the geographic isolation, and yet accomplishing the same evolutionary function. If one accepts the definition of sympatric speciation suggested above, this term would [26|27] not be applicable, however, to the just outlined conditions of speciation in the parasites (I have, of course, deliberately fixed the definition that way). Nevertheless, speciation in some parasites may occur under really different conditions from other non-parasitic forms, and I can only hope that this topic will be discussed by someone better qualified than myself.

Cordially,
Th. Dobzhansky

[end of *Bulletin 3*]

BULLETIN NO. 4

NOVEMBER 13, 1944

Contents

Introductory Remarks. Simpson[, p. i¹¹⁴]

1. Antiquity of disjunctive groups, plants and *Drosophila*. Stebbins to Mayr, p. 1.
2. Evidence on age of discontinuities in distribution of *Drosophila*. Mayr to Epling, p. 4.
3. Climatic changes in the Pleistocene. Colbert to Mayr, p. 10.
4. Reply to Mayr's criticisms of Epling's interpretation of *Drosophila* distribution. Stebbins to Mayr, p. 12.
5. Further discussion of *Drosophila* distribution. Mayr to Stebbins, p. 17.
6. Rates of evolution in plants. Elias to Dobzhansky, p. 21.
7. Comment on evolutionary rates in *Crepis*. Babcock to Elias, p. 26.

[cover page |i]

Introductory Remarks¹¹⁵

On returning to scientific pursuits after military service overseas, I am delighted to see how much has been accomplished by the committee of which I have been, until now, only nominal chairman. This series of bulletins, compiled and edited by Dr. Mayr who continues this task, has accomplished a great deal more than the expression of a few facts and opinions, useful as these have also been. From the whole series of letters in the bulletin there has emerged concrete evidence that a field common to the disciplines of genetics, paleontology, and systematics does really exist and this field is beginning to be clearly defined. Some, at least, of the more hopeful approaches to these common problems are indicated and exemplified. The existence of geneticists, paleontologists, and systematists interested in these problems and competent to attack them has been demonstrated. Their interest has been stimulated and made more concrete and their competence in the joint field has been increased by the exchange of views with students of other specialties. Thus great progress toward the goal of the committee has been made.

For the present, it is planned that the exchange of letters, as compiled in these bulletins, continue and it is suggested that this be broadened to

114. Pages "I" and "ii" are hand-numbered on Simpson's copy of this document.

115. Simpson returned to Manhattan from military service in August 1944 (see Simpson to Parr 25 August 1944, AMNH Archives, box "1186.1, 1944-1947," folder "G-Z 1944, 1186.1") and became active again in Committee business by mid-October. Following a 19 October 1944 note from Bucher to Mayr, Mayr wrote to Simpson suggesting a meeting of the Steering Committee "to discuss the future of the committee." Both notes in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1."

include the several students who have so far taken relatively little part. A list of those concerned was given at the end of the first bulletin, and suggestions for additions to this list will be welcome. As before, one copy of the letters (preferably the original) should be sent to Dr. Mayr. In the meantime a more concrete statement of the final aim will be sought by the steering committee and further definite plans laid.

This issue of the bulletin is largely devoted to letters by Stebbins and Mayr discussing a problem of rate of evolution, arising from Dobzhansky and Epling's [1944] monograph on *Drosophila pseudoobscura*. The fundamental problems involved include methods of evaluating and coordinating evidence from numerous different fields, the type of problem specifically within the scope of this committee. In more detail, it appears that the work of some botanists and [i]ii geneticists suggests an antiquity for certain floral and genetic types that is at variance with inferences drawn by some zoological systematists and paleontologists. Colbert has added pertinent evidence that climatic zones and correlated faunal and floral distributions did in fact change rather radically in the Pleistocene. Considerably more evidence could be adduced to show that many details of the biotic distributional pattern in North America are of quite late date. (Among many others, see, for instance, the recent important study by Hooper on rodent speciation in the San Francisco region in [Hooper 1944].) This may suggest a fruitful and interesting topic for further discussion.

Although not directly on the same subject, Elias' interesting letter and the shorter comment by Babcock have a strong bearing on the same type of problem. It is demonstrated that among plants there are great differences in rates of evolution (and also of distribution), both as individual rates of different lines within groups and as average rates of different groups. There is evident danger of overgeneralizing from atypical rates or of assuming some particular rate when the evidence is, at best, indirect, and this may be involved in the difference of opinion shown in the preceding letters. The same sorts of complex differences in rates are even more clearly demonstrated by groups of animals for which there is direct paleontological evidence on rates of evolution.

These and the many other problems involved in this exchange of views ramify so widely that they bear on the work of every member of the committee and may be a point of departure for some further correspondence.

G. G. Simpson [ii]1]

July 25, 1944

Dear Dr. Mayr:

One of the problems which in my opinion should be considered by our committee is that of the relation between the indirect evidence provided

by the present distribution of plant and animal groups for the rates of past evolutionary divergence, and the direct evidence on divergence which the fossil record gives us when it is available. As a botanist who has spent some time considering this type of evidence, I should like to know what you, as an authority on animal distribution, think of the type of evidence and the line of reasoning used by plant geographers, and also what if any evidence from animal distribution you would consider valid in relation to the past divergence of animal species and genera.

I bring this subject up partly as a result of reading in *Science* [Mayr 1944] your review of Dobzhansky and Epling's recent monograph on *Drosophila pseudoobscura*.¹¹⁶ In particular, I should like to know for what reasons you consider as "highly unlikely" Epling's conclusion that the inversion types of *D. pseudoobscura* with highly discontinuous ranges were in existence in Miocene time or perhaps earlier. The significance to a botanist of Epling's conclusion is that it was arrived at partly through indirect correlation with the geological and climatic history of western North America, and partly by means of a direct correlation between the distribution pattern of certain plant groups and the *Drosophila* inversion types in question. I am therefore anxious to know whether you consider as "highly unlikely" only Epling's interpretation of the correlation between the distribution of *Drosophila* and that of the plants, or whether you also question the interpretation of the history of the plant groups in the light of past climatic history and fossil floras.

If you do not accept the latter, you question a type of evidence which is admittedly indirect, but which has been considered valid by botanists [1|2] since the days of Darwin's contemporaries, and which seems to be backed up more and more strongly by the increasing amount of paleobotanical evidence that is available. If you disagree, therefore, we should like to know why, so that we can revise our thinking if necessary. And those who accept this distributional evidence must also accept conclusions which are in themselves rather startling. Take for example, the best known case of similarity of floras in widely disjunct areas; that between eastern North America and eastern Asia. I have been assured by Dr. Chaney that in the case of all plant groups which

116. Mayr's (1944) review of Dobzhansky and Epling (1944) provoked heated correspondence, culminating in a set of papers on the subject collected as a symposium in *Lloydia* as Mayr (1945), Stebbins (1945), and Simpson (1945a). Mayr proposed formally publishing their views to "stimulate other students to search for evidence pro and con and thereby help in the final solution of the puzzle" (Mayr to Stebbins 1 November 1944 in Mayr Papers, folder 105). Mayr claimed this exchange was "the first published evidence of the concrete work of our committee" (Mayr to Simpson 4 April 1945 in Mayr Papers, folder 120). Though Mayr's discussion of *Drosophila* may seem odd for an ornithologist, he had been commenting on *Drosophila* speciation as early as 1941 (Mayr to Gordon Mainland 4 April 1941 in Mayr Papers, folder 82) and was engaged in *Drosophila* research during the summers of 1943 and 1944 at Cold Spring Harbor as a collaborative project with Dobzhansky. That work involved behavioral isolating mechanisms between *D. pseudoobscura* and *D. persimilis*, see Dobzhansky and Mayr (1944; 1945; 1946a; 1946b) and Cain (2002).

show this disjunct distribution the common ancestor or ancestors of the group must date back to before the Miocene epoch. This statement is also made by Berry in his "Tree Ancestors" [Berry 1923]. Yet included among these groups are not only many long-lived trees and shrubs, but also perennial and even annual herbs. Furthermore, although in nearly all of the genera of trees and shrubs which show this distribution the species found in Eastern America are markedly distinct from the Asiatic ones, certain species of herbaceous plants are identical or nearly so in the two areas. For instance, in a paper by M. L. Fernald [1929] you will find listed as having this disjunct distribution *Symplocarpus foetidus* (L.) Nutt., the skunk cabbage, *Cypripedium arietinum* [sic: *arietinum*] R. Br., *Polygonum virginianum* L., and an annual species, *Polygonum arifolium* L. If we accept this geographical evidence, we must conclude that the American and Asiatic populations of *P. arifolium* have been isolated from each other for at least thirty million generations without diverging enough so that trained systematists can recognize any differences between them. Furthermore, the genus *Polygonum* contains about 275 species, many of them aggressive, plastic and evidently recent, indicating active evolution in other sections of the genus up to modern times. To one who must either accept this conclusion or reject a widely accepted and apparently valid type of evidence for evolution, Epling's conclusions about *Drosophila pseudoobscura* do not seem unlikely. [2][3]

Furthermore, the plant groups which shows disjunct distributions similar to that of the Santa Cruz and other inversions of *Drosophila* include not only the species of *Mahonia*, *Cupressus*, and *Chimaphila* mentioned by Epling, but also "paired" species or species groups in *Gaultheria*, *Baccharis*, and *Ceanothus*, a section of *Rhus*, the genus *Comarostaphylis*, and probably others. In many of these examples the possibility of recent distribution from California to Mexico or vice versa is unlikely because the plants concerned do not have a ready means of rapid dispersal over long distances, and more particularly because the differences between their modern representatives in the two areas are too great to be accounted for on the basis of recent divergence. This of course, makes them somewhat different from *Drosophila*, but no more so than the differences among the Eastern American-Asiatic series of plant groups such as that between the behavior of *Prenanthes*, a genus of perennial herbs in which species divergence since the time of isolation has been rather great, and the above mentioned *Polygonum arifolium*. I believe that as applied to the plant distributions, Epling's evidence against a Pleistocene dispersal is valid.

If you accept as valid the evidence for evolutionary divergence from the modern distribution of plant groups, but reject any interpretation of a causal relation between distributional patterns of plants and similar or identical ones of animals such as *Drosophila*, can you explain why, and

what substitute interpretation or interpretations you have to offer? It seems to me that the more nearly we can understand the relationship, if any, between the distribution patterns of plants and those of animals, the firmer will be our basis for the interpretation of distributional evidence for evolution as a whole.

Yours very sincerely,
G. Ledyard Stebbins, Jr. [3|4]

July 28, 1944

Dear Dr. Epling:

When the Committee on Common Problems of Genetics and Paleontology was organized, it was stated specifically that one of its functions should be to gather data on the rate of evolution. In this connection your recent publication entitled "The Historical Background [of the chromosomal races of *Drosophila pseudoobscura* and *Drosophila persimilis*]"¹¹⁷ is of the utmost importance. You investigate in this work the distribution of the various gene arrangements of these two species as correlated with the geography and paleoclimatology of the American West. After thorough consideration of all the available evidence you arrive at the conclusion (p. 176) "that not only [the] Santa Cruz [gene arrangement], but also its derivatives of the second and third degree, Tree Line, Cuernavaca, Olympic, and Oaxaca, were in existence during Miocene time or perhaps earlier. We advance this as an hypothesis and from it suggest a tentative history of the species." The detailed documentation of this thesis is presented in the above mentioned publication [Dobzhansky and Epling 1944], and I do not need to repeat here. However, in a recent review in "Science," I have referred to your hypothesis as a "highly unlikely conclusion." [Mayr 1944] Limitations of space in a book review prevented me from giving at that occasion a full statement of my reasons. It seems to me, however, that I owe you such a statement and that the bulletins of our committee are a proper medium for its presentation. At any rate a continued discussion of this important subject seems highly desirable.

Before stating the problem I want to emphasize that the facts are not under discussion in the consideration of your hypothesis but rather their interpretation. Each one of the arguments quoted by me in the following paragraphs is known to you but evaluated differently. The reason perhaps is that I have worked with insular faunas for the past 17 years while you have worked with continental floras. [4|5]

The facts are as follows: Chromosomal breaks may lead to inversions which can be detected easily by cytological methods. There is

117. Except for the citations, the [] brackets in this paragraph are not by Cain. They probably were inserted by Mayr to complete the title of the work (Epling 1944).

strong genetic evidence that all the flies that are the carriers of a given inversion are the descendants of a single individual. All the flies with the same gene arrangement are thus of common origin, and if they are now found in widely separated regions, some explanation must be found for such a discontinuity of range. For example, Cuernavaca, Santa Cruz, and Tree Line are found both in the Mexican highlands and in Guatemala but are presumed to be absent from the hot lowlands of the isthmus of Tehuantepec [*sic*: Tehuantepec], a distance of several hundred miles. Likewise, Santa Cruz is common in California and most of Mexico, from Chihuahua south-eastward, but seems absent from the arid Sonora-Arizona belt. There are a number of other similar discontinuities.

The questions that must be asked are: "What has caused these discontinuities and how old are they"? My conclusion that these discontinuities are of rather recent origin (not earlier than Pleistocene) is based on an evaluation of the data, which differs considerably from yours.

(1) *The selective value of gene arrangements.* You state (l.c. p. 147): "that, so far as known, the gene arrangements are attributes which are equal in selective value." To me the facts seem to indicate the opposite. To be sure, the inversion as such, that is the gene arrangement in the literal sense, is without selective value. However, at each locality the gene arrangement has a given gene contents and there is no reason whatsoever to assume that such local gene contents should be immune from selection. Consequently I have no doubt that the gene contents of the Santa Cruz arrangement are quite different in Guatemala, in Chihuahua end [*sic*: and] in southern California. In each case it has been modified by local selective factors. It is therefore not permissible to conclude that the gene arrangements Tree Line and Santa Cruz are without selective significance because they occur in two regions climatically as different as are British Columbia and Guatemala. Actually the Santa Cruz arrangement [5|6*] of British Columbia probably has a gene contents [*sic*] which is fundamentally different from that of Guatemala. This is obvious not only from the general theory of selection, but also from the more direct evidence of Dobzhansky's discovery of a regular seasonal fluctuation of Standard and Chiricahua at two localities in the San Jacinto Mountains. One can not escape the conclusion that the two mentioned arrangements have become associated at these localities with certain genes which influence their selective value at different seasons.

I am not prepared to suggest that selection has succeeded at each locality to incorporate a set of genes in each gene arrangement which makes the arrangement "perfectly" adapted. Inversion has undoubtedly reduced the frequency of crossing over and this is probably the reason why locally one gene arrangement may be superior to another. The Chiricahua arrangement, for example, seems to thrive in the arid Sonora-Arizona section where the related Santa Cruz arrangement is absent. Santa Cruz, on the other hand, occurs north and south in the more humid regions of the

Mexican plateau and of western California. Apparently neither the Californian nor the Mexican Santa Cruz arrangements have so far succeeded in incorporating in their gene contents mutations which would enable them to invade the intervening arid belt. The existence of clines in the frequency of certain gene arrangements also suggests that the adaptability of a given gene arrangement is not without temporary limits.

(2) *The Pleistocene Climate*. In your attempt to trace the origin of the discontinuities you present a thorough paleoclimatic history of the American West, by far the best summary in this field that has ever been attempted. This survey is of the greatest value to any paleontologist or student of Western American faunas. The main conclusion of your analysis is that the Pleistocene climate was not radically different from the present one and "that even during the pluvial periods the biota of the Pacific coast was separated from that of the Rocky Mountains by a relatively arid Basin and Range Province." This conclusion is well substantiated, the question only is, how arid is "relatively [6|7] arid"? There seems to be no doubt that even at the height of the Pleistocene pluvial period the central basin was relatively more arid than the coastal strip. On the other hand, can a period be called arid during which muskox lived in the Guadalupe Mountains and tapir in Arizona? Furthermore, if arid belts impede the spread of Santa Cruz and other gene arrangements, the question really is, were there any humid spells during the admittedly rather arid Pleistocene which could have been utilized by the gene arrangements to bridge the gaps? You doubt this possibility since in such a case one would "expect traces in the intervening region" if the population once had been continuous. This argument, of course, becomes invalid as soon as one admits that the gene contents may give a gene arrangement a local selective disadvantage. Counter selection may wipe out a gene arrangement as a consequence of its locally unfavorable gene contents.

(3) *Dispersal*. Your discussion (p. 151–160) implies that you consider neither active migration nor passive transport by wind as factors of much importance in the explanation of the distribution patterns of the gene arrangements. To me the opposite seems true. As far as active migration is concerned, Dobzhansky's and Wright's work has shown that the mean dispersal of a *Drosophila pseudoobscura* population is easily 1 kilometer per year (l.c., p. 43). This is an average distance "and some individuals will undoubtedly move farther and others much less far from the starting point." If a given gene arrangement had no selective value, it should spread at the rate more or less of one kilometer per year over areas suitable for the species. In this manner the gap between the Santa Cruz arrangements should be bridged in less than 1,000 years.

In this connection it must be emphasized that the gap between the Californian and the Mexican Santa Cruz areas is not a gap between species. On the contrary the gap is filled by flies with Standard, Arrowhead, Pikes Peak, and Chiricahua arrangements, all of which are viable

in heterozygous pairings with the Santa Cruz arrangement. The gap in Santa Cruz can thus by no means [7|8] be put in the same class as those found in the ranges of humidity loving plants like *Chimaphila umbellata* or *Mahonia fascicularis* [*sic*: *fascicularis*], which can not overcome the barrier of the arid southwestern desert. This fact is also important in connection with a consideration of passive aerial transport. Any Santa Cruz fly blown into the intermediate zone will at once be provided with a potential mate with a different gene arrangement. The fact that Santa Cruz is not found there, in spite of these favorable circumstances, indicates again that the gene contents of Californian as well as of Mexican Santa Cruz are of inferior survival value in the arid belt.

It would be a sterile discussion, if I would question your conclusions, Dr. Epling, without attempting to replace it by a hypothesis of my own. My own conclusion is that the present distributional pattern of the gene arrangements of *D. pseudoobscura* can be considered as of recent, that is of late Pleistocene or post-Pleistocene origin. I base this conclusion primarily on two sets of facts. The first is the adaptation (by selection) of the gene contents of each arrangement to a given locality. This provides for a dynamic means of adjustment to local conditions as well as for the elimination of gene arrangements locally from regions for which they do not possess well adapted gene contents. Major barriers are overcome by aerial transport, the all-importance of which has been shown for all regions with insular habitats (Gulick, Darlington, Zimmerman, etc.). A ten hour drift of a gravid female from Chihuahua to southern California will be sufficient to account for the original establishment of Santa Cruz in California. Such single colonizations [*sic*] might take place during heavy storms that have a different course from the prevailing winds. The jumping of the gap at the isthmus of Tehuantepec also can be best explained by aerial transport during a period of slight lowering of the life zones. It is now well established that this method of colonization gives the most plausible explanation for the occurrence of temperate zone faunas and floras on mountains in all tropical regions. [8|9]

To sum up, the problem of the discontinuities in the gene arrangements of *D. pseudoobscura* is much less one of establishment than [*sic*] of maintenance. The means of dispersal of *D. pseudoobscura*, both active and passive, are sufficient to account for a fairly rapid spread of all gene arrangements, provided they are favorable. The absence of a phylogenetically old gene arrangement from a certain region thus indicates that this gene arrangement is not provided with a gene contents of favorable survival value in that region. The distribution pattern of the gene arrangement is thus dynamic and constantly shifting with ecological conditions. It is controlled by the frequency of favorable mutations and of crossing over.

So much for the distribution of the gene arrangements. The question of the age of the arrangement is in my opinion only loosely

correlated with the age of the distribution pattern. To be sure, a gene arrangement with a very restricted distribution, such as Hidalgo, Cochise, Texas and San Jacinto, is probably of comparatively recent origin. On the other hand, the distribution gives no clue whether such widespread arrangements as Standard, Tree Line, and Santa Cruz originated 1,000 years ago or in mid-Pleistocene or in mid-Tertiary. The only clue as to the age of the "old" arrangements, that I can perceive, is the fact that the Standard arrangement is found both in *D. pseudoobscura* as well as in *D. persimilis*. This indicates that this arrangement is older than the split of the *pseudoobscura-persimilis* ancestor into two species. However, this is a rather barren discovery since we have no information whatsoever on the date at which this split took place. On the basis of our knowledge on the evolution of island insects, I suggest early Pleistocene or late Pliocene as the most likely date.

Sincerely yours,
Ernst Mayr [9][10]

August 29, 1944

Dear Dr. Mayr:

I have read the paper by Dr. Epling with a great deal of interest, particularly that part dealing with the past history of western North America. Certainly he has made a most thorough and useful summary of the climate and ecology that prevailed during Cenozoic times in this region, and this summary will be of inestimable value to students of past life on the Earth.

It is rather difficult for me to discuss Epling's paper at the present moment, because I am separated from the literature that I would like to consult before making any comments. For this reason what I have to say will be limited and rather general.

In the main, I have two criticisms to make as to his interpretations of the evidence—criticisms which have already been raised in your letter to Dr. Epling. In the first place I imagine that wind currents were far more important in the distribution of *Drosophila* during late Tertiary and Pleistocene times than Epling admits. Secondly I have the feeling that conditions in western and southwestern United States were not always as arid as Epling maintains. I have no background for discussing the first of these criticisms, so I will confine myself to the second.

With regard to the Pleistocene, Epling states that "glacial climates are relieved to have been either approximately as at present or wetter and somewhat warmer." I need not stress the point that the periods of glacial advance are generally considered to have been times of cold, arid environmental conditions, while the interglacial periods during which the ice was retreating, were generally warm and moist. Of course each

glacial advance and retreat had characteristics peculiar to it, but the generalizations made above are in the main valid.

It would seem to me that during the warm, moist interglacial periods conditions in southwestern United States might have been sufficiently favorable [10|11] as to allow the spread of *Drosophila*. This question occurs to me: would climatic and ecologic conditions that allowed horses and other grazing mammals to live in great abundance have been favorable to the spread of certain lines of *Drosophila*? There is no getting around the fact that at times during the Pleistocene period the southwest was able to support great herds of horses, and in addition such animals as the southern mammoth, ground sloths, camels and antelope. There must have been in those days grassy plains where there now exist deserts.

That the southwest was more humid in the recent geologic past than it is at the present is indicated by recent discoveries and studies made upon fossil mammals from that region. I might mention the muskox described from Williams Cave in the Guadalupe Mountains, associated with a fauna that is very late Pleistocene or post-Pleistocene. Probably this represents an assemblage living at or near the beginning of the last glacial retreat.

Recently I have studied and described a fauna associated with relics of Early Man in Arizona. This study is as yet unpublished.¹¹⁸ The site is Ventana Cave, in the southern portion of the state, a region which at the present time is very dry. Here, in association with flints, were found abundant remains of horses and other grazing mammals; also Say's Ground Squirrel, which at the present time does not extend south of the Gila River and which is found in open pine woodlands. But what is especially interesting is the discovery of tapir at this site.

We can not justifiably maintain that tapirs of perhaps some 20 thousand years ago were different in their habits and ecologic preferences than the tapirs of today. Therefore it is reasonable to believe that if there were tapirs in southern Arizona at that time, the climate must have been moister and the ecologic conditions somewhat different than they are at the present time. It seems to me that it must have been a savannah country, with streams bordered by trees, rather than the desert that it is now. [11|12]

I might say that this evidence for a moister climate in the southwest during the recent geologic past is corroborated by the evidence of Sandia Cave and certain other sites lately investigated.

How does this affect the problem of *Drosophila* distributions?

I sincerely trust that these remarks may be of some help to you.

Yours,

Edwin H. Colbert

118. This paper was not published, though Colbert (1989: 263–266) hints at such research, and Colbert (1942b; and 1947b) offer related studies. At the time, Colbert's research program was in transition: from mammals (e.g., Colbert 1942a) to dinosaurs (e.g., Colbert 1947a; 1947b; 1947c).

September 1, 1944

Dear Dr. Mayr:

Your letter of July 28th to Dr. Epling answers clearly one of the questions which I asked in mine to you of July 25. You apparently question only the validity of Dr. Epling's hypothesis that the similar distributions of the inversion types of *Drosophila pseudoobscura* and of certain plant species have had a common origin in terms of geologic history. Since, however, some of the evidence which you present seems to me in favor of rather than opposed to Dr. Epling's hypothesis, and since in the statement of your own alternative hypothesis you do not refer to Dr. Epling's arguments against this same alternative, more discussion of the question is in order.

In the first place I should like to give my opinion of your three points in the evaluation of the data.

(1) *The selective value of gene arrangements.* You should note that Dr. Epling's statement on page 147, which you quote, is followed by a reference to Part II of the monograph and that it is therefore, not his own conclusion, but a premise which was taken from Dobzhansky's results. The sentence which bears most directly on this point is on page 114, and states "the most plausible view is that in certain populations genetic variants which determine the fitness of their carriers have become, by chance, associated with certain gene arrangements [*sic*]". This agrees with your conclusion, but Epling's statement referred clearly to the arrangements themselves, not to associated gene complexes. [12|13*] As a matter of fact, the assumption of a different selective value for individuals possessing different gene arrangements seems to me not only favorable, but almost essential to the validity of Dr. Epling's hypothesis. There is little doubt that the discontinuity of the plant species groups mentioned is due to the fact that they are not adapted to the continental climate of the intervening area. Unless a similar assumption can be made in regard to the gene complexes of *D. pseudoobscura* associated with the gene arrangements having similar ranges, a similar origin of the two sets of distributions is difficult to postulate.

(2) *The Pleistocene Climate.* The discussion which you present here could be taken as an argument in favor of the continuous distribution of the Santa Cruz phylad from California to Mexico during the Pleistocene rather than the early Tertiary as postulated by Dr. Epling. This is not, of course, the same alternative explanation as the one which you favor in the conclusion of your letter, namely that of long distance dispersal in recent time, but nevertheless deserves the consideration that both you and he have given it. It seems to me, however, that when your evidence for a mild, relatively moist Pleistocene climate in the critical intervening areas of southeastern California, Arizona, New Mexico, and northern Mexico is compared with his in favor of an arid climate for the same

region during this epoch, the latter is more impressive. You cite records of the tapir in Arizona; he cites the clearly xerophytic flora and fauna of McKittrick, California (p. 164) and the conclusion of Meinzer, after a careful study of lake basins, that the critical region mentioned above was similar to southern Oregon and Nevada at present (p. 163). These latter regions most certainly are too arid and continental in climate to support the plant groups which have discontinuous ranges similar to those of the Santa Cruz phylad. Hence if the present discontinuity is caused by the lack of adaptation of this phylad (except for Chiricahua) to the arid continental climate, Epling correctly assumes that the evidence of Meinzer favors the hypothesis that this discontinuity persisted throughout the Pleistocene. However, [13|14] more evidence on Pleistocene floras is needed, particularly from Arizona and northwestern Mexico, before either concept can be accepted without reservation.

(3) *Dispersal*. Your discussion here seems to me somewhat irrelevant. It is obvious that in a few hundred or thousand years a succession of descendants from one individual of *Drosophila* could progressively traverse the distance from California to central Mexico or vice versa, provided that the intervening regions were favorable to them. The same may be said of the plant groups involved, except that here the dispersal could be even more rapid. In both cases, however, one legitimately asks the question "why the discontinuity, if such active migration is possible." If Santa Cruz is, as you suggest, "of inferior survival value in this arid belt", how could it have persisted there for the thousands of generations necessary to convey it by active migration from Mexico to California? The fact that in *Drosophila pseudoobscura* races rather than species are involved seems to me also irrelevant, if one assumes that these races, i.e., the gene complexes associated with the inversions, have differential survival values. In a number of plant species, as has been shown by Turesson [e.g., 1922], as well as by Clausen, Keck and Hiesey [e.g., 1939; 1940], there are ecotypes, or races, adapted to such habitats as sea beaches or alpine summits, which have discontinuous distributions, although the intervening area is occupied continuously by different races of the same species.

Your own hypothesis is presented as new, although it had already been carefully considered and rejected by Epling (pp. 150–153). It seems to me that his reasoning here is good, and I should like to know your opinion of it. If, as you say (and I agree is most likely), Santa Cruz of Mexico is different in the selective value of its associated genotype from Santa Cruz of California, how could the eggs and larvae deposited by the gravid Mexican female which you postulate live and grow in California in competition with the large populations of well adapted *D. pseudoobscura* individuals already present? Even if the adaptiveness is the same, the chances are certainly small that the few descendants [14|15*] of one stray individual could build up a sizeable population.

The analogy which you make to the colonization of insular areas by transoceanic migration is weakened by the fact that in the latter cases the migrant upon arrival meets no competition from members of its own or related species, while in *Drosophila pseudoobscura* of Mexico or California this competition would be very great.

To summarize. The discussion in your letter does not add to the three explanations which Dr. Epling cites in the last paragraph of page 150 of his monograph. Furthermore, you have not discussed any of his reasons for rejecting the explanations which you accept, and much of the evidence which you cite can be interpreted as favoring his explanation rather than yours. In view of these facts I, who felt after studying carefully Dr. Epling's paper that the evidence favored his explanation, have not found any reasons for changing my mind. This view is strengthened by the fact that other evidence from plant distribution, as stated in my last letter, indicates that some plant species, even including annuals, may possess remarkable evolutionary stability for long periods of geologic time.

Nevertheless, none of the three possible alternatives: a) long distance passive dispersal in recent time, b) active dispersal during a period of favorable climate in the Pleistocene, or c) origin and dispersal during the early part of the Tertiary periods can be definitely accepted or rejected at present, although the sum of available evidence seems to me to favor the latter. I should therefore, like to make a few predictions, which might serve as a guide to our evaluation of future evidence.

1. If Epling is correct, then fossil Pleistocene floras from southern California, Arizona, and northern Mexico, should in no case contain any of the plant groups or species pairs which now have discontinuous distributions similar to those of the Santa Cruz phylad, and fossil faunas should likewise show a scarcity or absence of animals preferring moist or heavily wooded habitats, with [15|16] a mild climate.

2. If Epling is correct, then a more detailed survey of gene arrangements in central California should show a relatively high percentage of the Santa Cruz arrangement in all of the regions possessing an ancient flora of southern affinity. At present, fig. 12 of Dobzhansky's part of the monograph (p. 127) shows high concentrations of Santa Cruz in three of the most important areas (Monterey, Santa Cruz Island, Cedros Island) occupied by the ancient closed cone pine forests, a group of plant associations containing a number of species with the central Mexican affinity. Collections in other areas of these forests, such as the coast between Fort Bragg and the Russian River, the vicinity of Inverness, the Santa Cruz mountains, Cambria, and Guadalupe Island, should also contain high concentrations of Santa Cruz. On the other hand, interior localities in the same latitude, such as Mt. Diablo, Mt. Hamilton, and Pinnacles National Monument, should show low concentrations of this arrangement.

3. If your hypothesis of long distance passive dispersal is correct, then the artificial establishment in the central California coast of flies

taken from central Mexico should be easy, and these flies should perpetuate characteristics peculiar to them for a period of years.

It seems to me that the importance of this problem lies not in the explanation of a peculiar set of distributional patterns, but in testing the possible validity of the evidence that a rapidly breeding, definitely mutating species like *D. pseudoobscura* can maintain evolutionary stability for millions of years. I hope therefore, that the discussion will go on, and that new evidence will come to light.

Yours very cordially,
G. Ledyard Stebbins, Jr.
[16|17]

September 8, 1944

Dear Dr. Stebbins¹¹⁹:

The determination of the exact age of the distribution pattern of the gene arrangements of *Drosophila pseudoobscura* is of the greatest importance to the student of evolution. I am therefore glad that you have once more focused attention in your letter of September 1 on some of the debatable aspects of the problem. Before entering a detailed discussion of the individual questions asked by you, I would like to state once more what the problem is.

The various gene arrangements (caused by inversions) that are known to occur in *D. pseudoobscura* are not scattered evenly over the range of the species, but each arrangement has a very definite distribution pattern. Most striking is that some of the ranges are discontinuous. Dr. Epling has come to the conclusion that the present distribution pattern is due to old historical causes and was already in existence "during Miocene time or perhaps earlier." I, on the other hand, contend that it is equally probable that the distribution pattern is due to recent or currently operating environmental factors, and that the latter hypothesis fits better with other evidence in the field of animal evolution. At any rate, the hypothesis of the recent origin of the distribution pattern is preferable because it is by far the simpler hypothesis. There are three main reasons which cause me to disagree with Dr. Epling's conclusions: (1) A greater emphasis on the fact that each gene arrangement contains a set of genes of specific survival value, (2) the fluctuating character of Pleistocene climate and in particular the recorded

119. In a letter to Epling several weeks before Mayr suggested "... it seems to me that [Stebbins' argument] is completely answered in my reply to you, and furthermore that Stebbins' entire argument is based on the wrong premises." Mayr asked Epling to encourage Stebbins to give a reply, adding "I entirely agree with you that new voices should be heard and have suggested to Dr. [Edwin] Colbert that he review the situation from the point of view of the paleontologist. After all, what we are after is to find facts and correct interpretations." (Mayr to Epling 14 August 1944 in Mayr Papers, folder 95) This disagreement helps explain the chill in Mayr-Stebbins relations later in the decade, when the two disagreed on publishing a manuscript in *Evolution* and when Stebbins' criticized Mayr's tenure as that journal's editor (Cain 1994).

occurrence of humid periods, (3) the great dispersal potentialities of *Drosophila* which will enable each gene arrangement to occupy suitable territory in a comparatively short period.

In your letter of September 1, you question the validity of my objections and state that I “do not refer to Dr. Epling’s arguments against [my own] alternative hypothesis.”¹²⁰ The three main points of my letter of [17|18] July 28 must therefore be discussed once more.

(1) The selective value of gene arrangements.

Dr. Epling’s account abounds with statements which indicate that he does not give any weight to the selective value of the gene contents of the various gene arrangements (p. 147, 148, 152, 153). This is a most crucial point because as soon as it is admitted, the distribution pattern can be explained by contemporary factors and does not need to be pushed back to the Miocene. For example, Dr. Epling states (p. 148), “The occurrence...in the most diverse climates of homozygotes of the wide-spread arrangements contradicts...the view...that they may have been segregated there by climatic factors.” This statement overlooks the fact that the “same” gene arrangement may have different gene contents (and hence different survival values) at different localities. To classify population [*sic*: populations] by the percentage occurrence of certain gene arrangements is open to the same objections that are valid against any other single-character classification.

On page 152, Dr. Epling reasons that winds could not be an essential factor in the dispersal of the gene arrangements because, “If Chiricahua and Standard could be carried eastward, why not Santa Cruz, which is an arrangement perhaps as ancient as Standard and certainly older than its derivative Chiricahua?” This reasoning again is based on the assumption of equal viability for the gene contents of all the different gene arrangements. My own answer to Dr. Epling’s question would be that Santa Cruz flies have probably been carried eastward as often as Standard and Chiricahua, but did not succeed in establishing themselves, because they lack something in their gene complement which would permit them to compete successfully with Chiricahua and Standard. By releasing Santa Cruz flies in the arid belt and recording the length of their survival period, some light might be shed on this question. Unfortunately, there are many potential objections to this experiment.

All of the questions posed by Dr. Epling on pp. 152–153 are much easier to answer if one assumes different selective values for the different [18|19] gene arrangements. Perhaps Dr. Epling himself came to a similar conclusion, for he concludes this paragraph with the following statement: “We cannot exclude the possibility that wind has caused the present distribution pattern in recent time. But the only tenable conclusion seems to be that, if such is the case, the factors are so

120. The preceding [] brackets in this paragraph are not by Cain, but probably by Mayr.

variable in effect that a consistent explanation is impossible at present.” (p. 153). I do not understand this last sentence unless Dr. Epling means that the environmental factors are different at every locality, which is, of course, to be assumed.

(2) *The Pleistocene Climate.*

Your implication that I believe in “a mild, relatively moist climate” does not agree with the statements made in my letter of July 28 where I speak of “the admittedly rather arid Pleistocene.” The Pleistocene, like all other geological periods, had a fluctuating climate. Arid cycles followed such with a more humid climate. I am perfectly willing to grant that the intermontane region was arid during the most arid phases of the Pleistocene and impassable for certain gene combinations of *Drosophila pseudoobscura*. The point, however, which is decisive is whether or not this area was equally impassable during the humid periods of the Pleistocene! I am not a paleontologist, but the evidence presented by Dr. Colbert in his letter of August 29 indicates to me that certain late Pleistocene or post-Pleistocene climates were so much more humid than the present climate that they should have permitted wide reaching range dislocations.

(3) *Dispersal*

I still can not see how Dr. Epling and you can homologize the distribution of the gene arrangements with that of species and races. In fact, you actually refer to them as “*Drosophila pseudoobscura* races.” The races or ecotypes of Turesson and of Clausen, Keck, and Hiesey are populations; the gene arrangements of *D. pseudoobscura* (which breed at random with other gene arrangements) are not. The important difference is that crossing over permits the exchange [19|20] of genes between the different gene arrangements [*sic*] while genic exchange is drastically reduced by distance between the plant races mentioned by you. I do not want to imply that the exchange of genes between the various arrangements is uninhibited, or else all gene arrangements would have similar distributions. The absence of Santa Cruz in the arid belt (where Chiricahua is common) indicates that inversions inhibit the amount of crossing over considerably. I do not know whether any genetic evidence is available which would permit to determine to what extent inversions impede crossing over. This is probably different in every combination, depending on the position of the breakage points, and on the length of the inverted section.

I agree with you entirely that the chance is rather small of a gene arrangement becoming established in a region where it was previously absent. The competition with other gene arrangements that are adapted to the specific local condition of such an area, is likely to be fatal. However, this does not eliminate the possibility that 1 in 1000 or 1 in one million of such colonization flights may be successful, because the

bearer of the arrangement happens to settle in a very localized, but eminently suitable niche. Numerous cases in the zoogeographical literature indicate that this probability is very real. Furthermore, there is always the possibility that a gene recombination which is actually inferior at its place of origin is "preadapted" in the sense of Davenport and Cuénot for life at a different geographical locality. In consequence I cannot see the necessity for assuming that every simple colonization flight, or better every passive long distance transport, will inevitably result in extinction. This statement at once answers your prediction (3). The artificial transfer of Mexican flies to central California (quite aside from the diagnostic difficulties) might succeed no more frequently than chance colonizations, certainly not every time. However, normal dispersal during favorable periods could close all gaps, even if one were to rule out long distance flights entirely. [20|21]

As far as your other two predictions are concerned, this is my guess:

(1) Plants with the same dispersal faculties as *Drosophila pseudoobscura* and with the same faculty of building up in a short time huge populations under favorable circumstances should be found in fossil condition in the intervening belt between their now disconnected ranges. Slowly maturing plants with heavy seeds can not be compared with *Drosophila*. It is now being realized with ever increasing clarity that zoogeography is not a science of former land (or habitat) connections but of dispersal faculties.

(2) If Californian "Santa Cruz" is (with minor local variations) a heat and humidity loving gene arrangement and if all the Californian "regions possessing an ancient flora of southern affinity" are the only parts of California possessing such a hot-humid climate, then nothing could be proved as to the age of the Santa Cruz distribution pattern. If, on the other hand, the survival of this ancient flora at the localities mentioned by you is due to factors of the dim past and not caused by the current climate, then a close association of Santa Cruz with these floras would indeed be indicative of the high age of these gene arrangements.

I hope that these remarks have helped to clarify the issue.

Yours very cordially,
Ernst Mayr¹²¹

June 28, 1944

Dear Dr. Dobzhansky:

Your letters to Doctor Chaney of February 5 and April 14, 1944, and the ensuing correspondence, which was mimeographed and distributed in

121. Mayr continued this discussion with Stebbins, see Mayr to Stebbins 1 November 1944 in Mayr Papers, folder 105.

Bull. 1, May 15, 1944, of the Committee on Common Problems of Genetics, Paleontology and Systematics, have helped considerably in focusing attention on the problems which confront the geneticists who attempt to evaluate the significance of the paleobotanical evidence for the study of evolution. [21|22]

Geneticists who seek contact with paleontologists, like yourself, Haldane and others, cannot help but realize that the genetical changes which they observe to occur naturally, or which they produce experimentally, are by themselves not enough to explain entirely the evolutionary changes observed in fossil organisms and revealed by Paleontology. The paleontologist has the advantage of being able to study evolution proceeding through millions of years, while the evolutionary changes observed by the geneticist cover only a few years or, at best, a life's time. Now you request a specific piece of information, namely the rate of evolution of plants in Cenozoic age, and you found that the paleobotanists working on arboreal Phanerogams are not quite prepared to answer this question. They do not know, as yet, how to differentiate on the available fossil bulk-material, the extinct species from those still living. Their differentiation, in by far the greatest number of cases, is still quite arbitrary and vague. Conflicting answers may be found even in a single statement: on page 5 (Bull. No. 1) it is said regarding Miocene floras that the "number of extinct species is so small as to be wholly negligible;" but on page 6 it is said that "plants of the Lower Tertiary (pre-Miocene) are even less readily referrable [*sic*] to living species than those of the Miocene," which implies that in Miocene extinct species were abundant. This could be considered a *lapsus calami* if it were not for the fact that a recently published statement on the subject by one of Chaney's school, reads thus: "In paleobotanical practice a plant from beds of Pliocene age or older is habitually referred to an extinct species, and given a separate name, no matter how similar it may appear to a living species. This implies that all living species have arisen since the end of the Tertiary, which may not be a fact." [LaMotte 1936]. Thus, it appears, that we still have only a general, vague impression, that the evolution of Angiospermic plants in Cenozoic age was so slow and so indefinite as to be practically negligible. However, as Doctors Babcock and Stebbins wrote to you already, this answer, if acceptable, [22|23] refers only to arboreal vegetation, while the evolution of herbs was quite different. The studies on *Crepis*, although based almost exclusively on living forms, are reasonably conclusive in claiming that only a few living species (two) originated in Miocene, and most are of much younger age. Of course, until a reasonably abundant and well preserved fossil species of *Crepis* are [*sic*: is] found, no exact knowledge of number of these species originating at a given geological time is possible. On the other hand, there are two groups of other herbs, the extinct species of which are known from well

preserved fossil seeds and were found in sufficient abundance to allow such judgment: these are the “*Water-Soldier*” (*Stratiotes*) and the spear-grass (*Stipa* and its kin). Fossil record[s] of a few other herbs (Borages, Cyperaceae and others) is being gradually built up, and will be soon available for similar evaluation.

The evolution of the *Water-Soldier*, the monotypic European and Siberian herbaceous water monocotyledon, was a subject of careful research by Miss M. E. J. Chandler [1923, p. 117]. She differentiated the fossil species on their seeds alone, which was also the practice in their differentiation by other paleobotanists who worked on the same seeds. According to her summary presented in the form of a chart on p. 124 there are 9 Tertiary species of *Stratiotes* known from the European rocks, which lived in the course of time from late Eocene to Medial Pliocene, and all are extinct. The single known living species of the genus, *S. aloides*, originated in late Pliocene time. It can be observed, on the same chart, that in the “Main Line of Evolution” of *Stratiotes* species succeeded species at an average rate of about one in six millions of years. Considering the fact that the *Water-Soldier* belongs in a special ecological niche, where there is comparatively little competition from a few other water plants, its slower rate of evolution compared with that of the prairie *Stipeae* (see below) seems understandable.

The study of the Tertiary herbs in America was put on a different basis than that generally used in the study of the Angiospermic fossil leaves. [23|24] The beautifully preserved fossil grass seeds were studied [*sic*] and illustrated in detail greater than that usually employed for the study of the corresponding parts in the related living herbs; in order to perfect comparison the living prairie herbs too were correspondingly studied and illustrated in as much additional detail as was necessary in order to prove their close relation to the fossil seeds. Fortunately, the parts of the seeds which were found as fossils: the protective covers (combination of lemma and palea) of the grain, and the nutlets of Borages, were already customarily used for specific differentiation of the living plants, in preference to (though not without connection with) other, readily observable parts, such as leaves, flowers, etc.

Besides being excellently preserved, the protective covers of grasses and borages were collected in sufficient abundance to observe variability in each collected sample of seeds, and in each established species. The systematic collection from scores of localities throughout the Tertiary mantle of the High Plains, from Texas to South Dakota, allowed, furthermore, to build an exact succession of the local herbaceous floras.

When this was established, ecological analysis was used in order to find which species were coming to and going from the area in the course of Tertiary time as the result of climatic changes; and after discounting these purely ecological appearances and disappearances, the remaining

succession of closely related species in the succeeding strata was attributed to speciation, that is to endemic evolutionary changes in the local herbs. Because the fossil grasses were collected in greater abundance than borages, their study was first completed so that their rate of evolutionary changes can now be reasonably established. On the evidence presented in the chart (Plate 17) of the "Tertiary Prairie grasses and other Herbs of the High Plains," [Elias 1942], one can conclude that the grasses of the tribe Stipeae, the species of which became dominant in the prairie, were evolving, in a single line of ascent, at a rate of one in about a fourth or fifth of the time embraced by Miocene, that is, one in about [24|25] 2 or 2½ millions of years.

On the other hand, judging from the seed covers (stones) of hackberry, which are very abundant in the same Tertiary rocks of the High Plains, there was no specific change in this tree since the end of Oligocene time. This conclusion is in harmony with the few data on leaves of *Celtis* though perhaps, judging by changes in the collected leaves, the hackberry which grew in the valleys was more mutable than that which was sparingly dispersed throughout the Tertiary prairie. Compared with the herbs the Tertiary trees were producing new ecologically dominant species at a rate 6 to 9 times slower, or one dominant species in about 15 to 20 millions of years. There is not a single known Tertiary species of the tribe Stipeae or of borages now living. All Pliocene species became extinct at the end of this time or sometime in the Pleistocene, probably in its early part. Of the seven known Miocene species of Stipeae only one survived into the early part of the Pliocene, where, on the other hand at least 10 known new species originated. Compare these numbers with about 600 species of living Stipeae, of which 84 are endemic to the United States (excluding Alaska).

The striking contrast of the comparatively rapidly evolving herbs and the conservative trees, as now revealed by the available paleobotanical record is in good agreement with the fact, originally pointed out by Sinnott (1914)¹²² and later emphasized by Arber (1919–1928),¹²³ that because trees begin to fruit on the average at the 20th year of growth, while annual herbs bring seeds each year, the evolution of the latter should go, on the average, faster in direct proportion to the frequency of successive generations.

Another important fact has been revealed by the fossil prairie record, now available: the first stipeae, known from the Lower Miocene, were already essentially very much like their living descendants, which means that grass acquired its essential characters and herbaceous habit (unless it was always an herb) while it was a part of undergrowth or (and) of forest margins. The [25|26] evolution of prairie

122. This reference is not clear, probably referring to Sinnott (1914a) or Sinnott (1914b).

123. This reference is not clear. Arber's work is represented by Arber (1928; 1950) and described by Thomas (1960).

grasses throughout the Miocene and Pliocene did not create any new features, but was that of reduction of some parts and modification and adaptation of others, chiefly for better protection against drought, and better dispersal of seeds.

Sincerely yours,
M. K. Elias

July 18, 1944

Dear Dr. Elias:

Thank you for the copy of your letter to Dr. Dobzhansky dated June 28. I am grateful for your summary of the evidence on the comparatively rapid evolution of the grasses of the High Plains during the Cenozoic. The history of *Crepis* is evidently similar even [though] I do not have much fossil evidence. In this connection I should like to point out that it is necessary to assume the existence of over 20 species of *Crepis* in Asia during early Miocene instead of two as mentioned parenthetically at the top of page two of your letter. The *two* species mentioned by me in Bulletin #1 page 11 are American species. But on page 13 of Bulletin #1 in my paragraph 3 it is stated "That the *most primitive* species of *Crepis* are very old (early Miocene)..." As a matter of fact there are 21 of these most primitive species, not counting the two American species already mentioned; and it is highly probable that these most primitive species were differentiated into geographical and ecological groups in early Miocene.

I mention this evidence to show that *Crepis* probably originated somewhat earlier than you seemed to think. But these most primitive species comprise only one tenth of the whole genus, whereas the remaining species are younger, many of them much younger. Thus the evidence from *Crepis* certainly corroborates your argument.

Sincerely yours,
E. B. Babcock

[end of *Bulletin* 4]

BULLETIN NO. 5¹²⁴

FEBRUARY 5, 1946

Unlike previous bulletins, this one is composed, not of letters by Committee members, but of information, plans, and proposals. It includes two very important matters on which the individual assistance of each member of the Committee is urgently needed: arrangement of a program for a conference and symposium, and proposals for foundation of a journal and a society in the field of the Committee. Early replies, by letter to the Chairman, will be much appreciated and will greatly facilitate the work of the Committee.

Progress and Plans of the Committee

As expressed in earlier reports, the purpose of this Committee is to further studies in the field designated by its name in three specific ways: (1) by meetings, (2) by correspondence, and (3) by a final conference involving a symposium to be published.

(1). War conditions have made a general Committee meeting impossible, but several local and steering committee meetings have been held. These have been noted in the annual reports and bulletins. The function of preliminary meetings has been adequately carried on by correspondence. It is now proposed that a definitive general meeting be held in connection with the conference, outlined on a later page. [1|2]

(2). Correspondence on problems in the field of the Committee has been circulated in four mimeographed bulletins. It had been planned to continue this for another year, but subsequent letters suggested that the usefulness of this activity had been rather completely exploited. It was essentially an exploratory mechanism and it assisted greatly in outlining the field and demonstrating the sort of contributions that could be obtained. Even during this preliminary period, there was considerable feeling that the contributions had wider and more permanent value than could be fully realized by circulation of unpublished material within the Committee. The next step should, then, be to provide for the continuation of this type of discussion in more permanent form and for a wider audience. Proposals to achieve this end are discussed later in the present communication. In the meantime part of the discussion in the Committee's bulletin has already been published, in revised and expanded form, as a "Symposium on the Age of the Distribution Pattern of the Gene Arrangements in *Drosophila pseudoobscura*" in Lloydia [Stebbins, et al. 1945].

124. The year-long break between *Bulletins* 4 and 5 is discussed in Appendix F, [CCP] Annual Report, April 1946 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3," and Cain (1994). Attention was focused on conference planning and creating the new society and journal.

(3). War conditions made it clearly inadvisable to schedule a general conference and symposium during the past two years. This is, however, practicable for 1946 and it is proposed immediately to start formulating definite plans. Suggestions and invitations have already been received for holding such a conference under the auspices of established institutions and organizations, and an alternative is for this committee to hold the conference independently. The possibilities are still being studied and no definite proposal can yet be made. Further suggestions as to time, place, and auspices will be welcome. The Committee as a whole will be notified and consulted before any decision is reached. [2/3]

Conference Program

Proceeding on the premise that a conference will be called later in 1946, it is necessary to proceed at once to the formulation of a definite program and selection of participants so that time will be available for preparation of contributions.¹²⁵ A general call for papers seldom produces an adequate, unified, and well-balanced symposium. It is therefore suggested that broad but definite topics be selected, that members of this Committee state what contribution they are prepared to make to the discussion of these topics, and that in addition we select individuals not on the Committee to be invited to make contributions on specified subjects.

Subjects treated or suggested in the correspondence, bulletin, and meetings of the Committee almost all fall under the following general topics:¹²⁶

1. Rates of evolution.
2. Evolutionary trends.
3. Discontinuity.
4. Geographic variation.
5. Adaptation.

1. It is clear from the activities of this Committee that the general topic of rates of evolution has evoked the widest response and has most fully involved all three of the fields of genetics, paleontology, and systematics. There is no question that this topic should figure largely in the

125. Part of the planning process is described in Simpson to Mayr 6 December 1944 in SSE Papers, box N-Sp, folder "Simpson, George Gaylord" and in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3."

126. The following assessment matches one a year before in Simpson to Mayr 6 December 1944 in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #1," with one exception. After describing the need to discuss adaptation, Simpson wrote about the need for another topic of discussion. "The other is the subject of what I have recently called the modes of evolution, a rather complex and synthetic subject since it involves almost all our previous topics and several others, but brings them together in a particular way. I do not know whether these subjects will prove especially fruitful for the Committee, but I would like to see them tried out. What I might contribute on them is largely summarized in my recent book, and I invite other members of the Committee to supplement or criticize this."

proposed conference and symposium. The questions are (a) whether it would be advisable to unify the symposium by confining it to this topic or whether others, too, should be included, and (b) in either case, what specific subjects under this general topic can be and should be considered.

2. Trends have several times been mentioned during the Committee's activities, but they have received little serious attention from us. The [3|4] topic would appear to be one on which geneticists and paleontologists, particularly, need to cooperate and it could well be on the agenda of our conference. If it is to be included, it will be necessary to formulate particular problems for attack, because simply mentioning the whole question of evolutionary trends does not seem to stimulate discussion.

3. The general topic of discontinuity has received considerable attention, but the results do not seem altogether favorable to inclusion of the topic in our symposium. The geneticists, paleontologists, and systematists have discussed quite different things under the heading of "discontinuity" and there seems to be a lack of clearly formulated and really common problems in this field. Explicit proposals of subjects that do represent problems of discontinuity common to two or all three of our fields would be welcome, but these have not emerged from our previous explorations.

4. There has been much mention of geographic variation in connection with rates and with discontinuity, but when geographic variation has been taken as a primary topic, it does not seem to have been dealt with as a common problem of our various fields. It therefore seems relatively unpromising as a separate topic for our symposium.

5. Adaptation, or more broadly the whole subject of the relationship of genetic constitution to physiology and morphology and of physiology and morphology to ecology, has hardly been mentioned in our previous discussions. This seems, nevertheless, so obviously a large and important topic involving the whole field of this committee that attention is now drawn to it and comment on it as a symposium topic is invited.

*Committee members are urged to fill out and return the enclosed blank as soon as possible.*¹²⁷ [4|5]

Proposal for a Journal and Society for Studies in the Committee's Field

As organized under the National Research Council, this Committee is temporary and is to be disbanded after it has fulfilled its short-range program of exploration and stimulation. It has been anticipated that this program would end with the proposed conference later this year. Part of the program is, however, to provide, if possible and advisable, for continued attack on the problems within the Committee's scope. This

127. A copy of this blank is located in Simpson Papers, folder "National Research Council (Committee on Common Problems...) #3." It is reproduced here as Appendix 6.

implies either placing the Committee on a different, continuing basis or transferring its functions to a permanent organization.

The most specific plan for continued activity yet proposed is the establishment of a journal devoted to general evolutionary problems and attacking these from the combined points of view of genetics, paleontology, and systematics. This proposal was originally made by Dr. Mayr, of this Committee, and he has informally discussed it with other committee members, with Julian Huxley, and others. There is no journal devoted to this field and the feeling of those so far consulted is that the subject is not adequately covered by existing biological journals. It seems highly probable that there is an audience for such a journal and that suitable papers of high quality would be forthcoming under the leadership of a vigorous editor. The major problems are sponsorship and financing.

The National Research Council has indicated [a] willingness for this Committee to sponsor such a journal and to solicit funds for that purpose. The solicitation of funds and the responsibility for them would, however, be up to the Committee and not to the Council. Some of the research foundations have been informally approached, and their unofficial reaction toward providing funds for this purpose was unfavorable. It seems unlikely that any [5] [6] substantial support from such sources will be available here in the near future, in part because of prior commitments for post-war assistance to British and other foreign scientific organizations. Financial support from individuals within the biological sciences would clearly have to involve a much larger group than this Committee, with its 30 members, while efficient editorial direction would have to be concentrated in a smaller group.

There is no doubt that this Committee could quite properly cooperate in and promote the foundation of such a journal, but there is [a] serious question whether it should, as such, act as sponsor with corresponding financial and editorial responsibilities.

In correspondence with Dr. Mayr, Dr. Huxley has indicated that there is great interest in starting a journal of evolutionary studies in England and that funds for this purpose would probably be available there. If the journal is initially published in England, it will nevertheless be explicitly international in character and it is proposed that publication may be transferred to America if political or economic difficulties should arise.

It is further suggested that a society be formed in this field and that dues, at least in part, be applied to journal subscriptions. This not only would serve to ensure wide distribution and continuing financial support for the journal, but also would promote continuous future attention to the field of our Committee. The Committee as such could thus be disbanded with the assurance that its work would go on, developed by the society on a much broader basis than is possible for a committee, alone.

Another suggestion is that the proposed society should take over, in a new and expanded organization, the functions of the now quiescent Society for the Study of Speciation ("S.S.S."). This Society, originally suggested by Dr. Huxley and promoted by Dr. Mayr, Dr. Dobzhansky, Dr. Alfred Emerson, [6]7 and others in this country was formed just before the war to promote studies and cooperation in a field similar to that of our Committee.¹²⁸ Its executive committee consisted of Edgar Anderson, [John Mann] Beal, William Burrows, [Leon Jacob] Cole, [Lee Raymond] Dice, [Theodosius] Dobzhansky, Alfred Emerson (Secretary), [Alfred Charles] Kinsey, [Wilton Marion] Krogman, [Ernst] Mayr, [Karl Patterson] Schmidt, [George Gaylord] Simpson, and Sewall Wright. (Five of these are members of this Committee; six other members of this Committee were members of the S.S.S.)

The S.S.S. issued several valuable mimeographed bulletins but it became quiescent during the war and evidently requires some reorganization and change of scope if it is to be reactivated. It did, nevertheless, reveal considerable interest in this field and it provides a possible basis for the proposed new society, whether the change be considered as a reorganization of the S.S.S. or as a merging of that Society into a new and broader organization. The S.S.S. still holds funds sufficient to cover expenses incidental to a reorganization or new organization such as is now proposed. The proposed society would not be confined to speciation, as implied by the name of the S.S.S., but would cover the whole subject of evolution, viewed as a synthesis from all pertinent fields. The name applied to it would reflect this broader, inter-discipline scope.

It is proposed that this possible rebirth or merger of the S.S.S., along with the general question of formation of a society and publication of an international journal in this field, be discussed at the forthcoming A.A.A.S. meeting at St. Louis by a voluntary committee including members of the executive committee of the S.S.S. and of our Committee on Common Problems of Genetics, Paleontology, and Systematics.

You are requested to give the benefit of your judgment and advice, particularly on these points:

(1) The establishment of an international and inter-discipline [7]8 journal for evolutionary problems.

(2) Methods of financing and sponsorship. The proposal for publication in England, if sufficient financial support cannot be secured in this country.

(3) The formation of a permanent society for studies in the field of this Committee.

(4) The conversion or merging of the Society for the Study of Speciation into this proposed society.

128. Cain (1999) reproduces the one news bulletin, address list and bibliography known to have been produced by the Society for the Study of Speciation. Cain (2000b) discusses the origins, activities, and failure of this group.

Reading Lists

Annotated reading lists in each of these three major fields of the Committee are appended to this Bulletin. The list of genetics has been compiled and annotated by Theodosius Dobzhansky [Appendix 3], that on Systematics by Ernst Mayr [Appendix 5], and that on paleontology by G. G. Simpson [Appendix 4].¹²⁹

Address correspondence to:

Dr. G. G. Simpson
The American Museum of Natural History
New York 24, N.Y.

[end of *Bulletin* 5]

129. In the October 1943 *Report of Meetings* (p. 9), these bibliographies were assigned to K. W. Cooper and Curt Stern for genetics and to Alfred Romer for paleontology. These were not completed and presently mentioned alternatives were provided to committee members.

BULLETIN NO. 6¹³⁰

MAY 6, 1946

Since circulation of the last bulletin, the annual report of the Committee has been prepared by the chairman and submitted to the N.R.C. at its annual meeting, 3 May, 1946.¹³¹ Mimeographed copies will be circulated by the Council to members of the Committee. The subjects covered are already known to you or are discussed in more detail in the present bulletin. The most important matters now before us are our proposed conference and symposium and the organization of the new Society for the Study of Evolution.

Conference

The following invitation, addressed to this Committee through G. G. Simpson as chairman, has been received from G.L. Jepsen, as director of the proposed Princeton conference:

“...Princeton plans to sponsor a series of conferences during the 1946–7 academic year in celebration of its Bicentennial. One conference has been proposed and planned on the subject ‘Genetics, Paleontology, and Evolution.’ In recognition of the active and productive work in this general area by the N.R.C. Committee on Common Problems of Genetics, Paleontology, and Systematics, I am authorized to invite the Committee to cooperate in the Conference. Each member of the Committee and about twenty other scholars, some from foreign countries, will be invited by the University to participate as Conference speakers or members and to be its guests for a 3-day meeting on [1|2] January 14th to 16th, 1947 at the Princeton Inn. Princeton will contribute \$600 or more toward the travel expenses of American principal speakers and plans to arrange for the transportation of foreign speakers.

“It is fully recognized that the success of the Conference will be due to the previous pioneer activity and generous cooperation of the N.R.C. Committee. As Director of the Conference for Princeton I will ask Simpson and Dobzhansky and Mayr and

130. The source for *Bulletin 6* is NAS Archives, folder “Geology and Geography. 1946. Committee on Common Problems of Genetics, Paleontology and Systematics.” This is virtually identical with a carbon draft dated the previous day located in Simpson Papers, folder “National Research Council (Committee on Common Problems...) #6.” This draft contains Simpson’s hand-written note: “Ernst. For your criticism. If you find it OK, I’ll have mimeo’d + distributed. GGS.” In Mayr’s hand-writing, “O.K. EM.” It presents an issue date of 5 May.

131. Other correspondence relating to Committee work at this time and in the transition to the Society for the Study of Evolution is located in NAS Archives, folder “Geology and Geography 1946: Committee on Common Problems of Genetics, Paleontology and Systematics.” At this point, Simpson also was involved in the Committee on the Application of Biological Methods and Data to Geological Problems.

Babcock and K. Cooper to serve with me on an Advisory Committee for the Conference. Cooper is also alternate director.

"Princeton University is planning to issue a small brochure of approximately twenty-four pages in the case of each Bicentennial Conference summarizing the discussions of the Conference and listing the members participating. It does not intend to publish any other proceedings of the sessions, and the N.R.C. Committee can of course make any arrangements it chooses for the publication of a symposium or proceedings of the Conference.

"On behalf of the Bicentennial Conferences I sincerely hope that this proposal will be favored by the National Research Council.

Sincerely yours,
(signed) Glenn L. Jepsen."

This proposal was discussed by Jepsen, and K. Cooper, for Princeton, and by Simpson, Dobzhansky, Mayr, and Colbert for this Committee. It seemed to us that this invitation gives an opportunity to stage a conference in our field under excellent auspices and conditions and can be considered an ideal way of carrying out our plans in this respect. The invitation was therefore tentatively accepted, subject to approval by the National Research Council and by this Committee as a whole. Formal approval has since been received from the Council, through W.W. Rubey. The approval of the other Committee members is now requested. [2][3]

The program has not yet been arranged, even tentatively, but it has been suggested that the three days available under the Princeton plan could involve seven or more leading addresses, each followed by shorter, prepared presentations of related material by two or three discussants and then by general discussion from the floor. If the Committee approves the plan for cooperation with Princeton, it is hoped that a preliminary program may be drawn up within the next few weeks by a joint program committee or group, tentatively proposed to include Jepsen, acting both for Princeton and for this Committee, K. Cooper, for Princeton, and Dobzhansky, Mayr, Simpson, and Babcock, for the Committee (and, by invitation, as advisors for Princeton).

Replies to the recent questionnaire on conference topics¹³² have been studied and will be used in drawing up the program. Most Committee members stressed rates, trends, and adaptation as suitable general subjects, and these may be taken as main themes, without necessarily excluding attention to some related topics in our field. Assuming, still, that the tentative plan for cooperation with Princeton in this way is acceptable to all our Committee members, it will be noted from Jepsen's letter that all will be invited to attend. In addition to

132. This questionnaire is reproduced here as Appendix 6.

Princeton's offer, it is anticipated that the National Research Council will provide some funds for travel expenses and this will permit paying a considerable portion, but perhaps not quite all, of these expenses for Committee members. In order to keep the program integrated, leading papers and formal discussions will be prepared by invitation, but the invitations will be made in the light of what has already been volunteered, and it is hoped that all Committee members will participate in the informal discussions. Some students who are not members of this Committee will also be invited to speak, and it is particularly hoped that these can include some of our foreign colleagues. [3|4]

Symposium

Under the proposed plan for cooperation with Princeton, manuscripts of papers and discussions presented at the conference will be turned over to the Committee, rather than to Princeton. In order to carry out its long-standing plan, the Committee would then assemble and edit these as a symposium volume.¹³³ If suitable material is available, this volume will also include some papers in addition to those presented at the conference. An opportunity will thus be given to include any work by Committee members that is in the field of the Committee but that may not fit into the more limited time and scope of the conference. The volume will constitute the final activity of the Committee and will be presented as its definitive report. It would be premature to consider definite arrangements [sic] for publication at this time, but this matter is being kept in mind not only within the Committee but also by the officers of the National Research Council.

The Society for the Study of Evolution

The Committee has previously been informed of tentative plans to have its work perpetuated by the foundation of a society to be devoted permanently to work in its field. Through the joint efforts of this Committee and of the executive committee of the former Society for the Study of Speciation, this plan has now been put into effect. The Society for the Study of Evolution was organized on 30 March 1946 at the St. Louis meeting of the American Association for the Advancement of Science. The purpose of the new Society is the promotion of the study of organic evolution and the integration of the various fields of biology. It thus includes the purposes of our Committee.

The officers for 1946–47 are as follows:

President:	<i>G. G. Simpson</i>
Vice-presidents:	<i>E.B. Babcock</i> , A.E. Emerson, J.T. Patterson [4 5]
Secretary:	<i>E. Mayr</i>

133. This plan culminated in Jepsen, Mayr, and Simpson (1949).

Treasurer: K.P. Schmidt
Council: E.R. Dunn, *H.J. Muller, G.L. Jepsen, S. Wright,*
Th. Dobzhansky, R.W. Chaney.

(Names [italicized] are those of members of this Committee.)

One of the purposes of the new Society is to edit a journal of studies on evolutionary problems, especially the sort of inter-discipline problems that have been the concern of our Committee. The plans for such a journal necessarily involve a larger, broader, and more permanent organization than the Committee, itself, and henceforth will be the concern of the Society rather than of the Committee.

The Society for the Study of Speciation has disbanded and its records and assets have been turned over to the Society for the Study of Evolution.

Dues for the first year of the Society for the Study of Evolution have been set at \$1.00, but members are invited to contribute an additional \$3.00, or more, to help build up a fund for support of the proposed journal. When the journal is being published by the Society, dues will include subscription to the journal and will then, of course, be higher, probably \$4.00 per year.

Members of this Committee are eligible for charter membership in the Society and it is hoped that all will join. Application and enquiries should be addressed to the secretary, Dr. Ernst Mayr, The American Museum of Natural History, New York 24, N.Y.

G. G. Simpson,
Chairman [5|6]

[Appended to *Bulletin* 6 was a two-page "Reading List on Paleobotany," reproduced here as Appendix 7.]

[end of *Bulletin* 6]

APPENDIX 1

Recruiting Letter for Committee

[Organizers of the Committee on Common Problems distributed this three-page letter while composing the Committee. The full list of recipients is not known, but it likely included those named in this letter. A 1 June 1943 report on these organizing efforts reported, “Enthusiastic replies were received from all the workers listed on the second page of this letter [Table A1.1], excepting those who had or were about to enter the armed forces.”¹³⁴]

[The original is located in the NAS Archives, folder: “Geology and Geography. 1943. Committee on Common Problems of Genetics and Paleontology.” It carries the typed letterhead: “National Research Council / 2101 Constitution Avenue / Washington, D.C.” Handwritten on the first page of this copy is “Copy for *Mrs. Best* / mimeographed in / New York for / Dr. Bucher / (M. L. Johnson)”.]

February 26, 1943

Dear Colleague:

Impressed with the valuable results that have come from the systematic cooperation of geologists and physicists, and geologists and chemists, Professor Bucher suggested in an address before the annual meeting of the Geological Society of America in December, 1941, that no less benefit might be expected from joint counseling of paleontologists and biologists. The suggestion was welcomed by a number of paleontologists and geneticists. As a result of discussions between individuals, the following group met around a table in the Library of the zoology department of Columbia University on the afternoon of October 17, 1942:

C. M. Balder	Glenn Jepsen
W. H. Bucher	E. Mayr
E. A. Colbert ¹³⁵	H. J. Muller
Th. Dobzhansky	A. S. Romer
L. C. Dunn	G. G. Simpson
	H. E. Wood

All present seemed agreed that the paleontologists should be better acquainted with the methods of working and especially the essential results of geneticists, and that the same is no less true, vice versa, concerning the degree of reliability obtained by stratigraphic and

134 “Report of the Committee on Common Problems of Genetics and Paleontology,” 1 June 1943 in Simpson Papers, folder “National Research Council (Committee on Common Problems...), #1.”

135. “E. A. Colbert” is an error. The name is Edwin Harris Colbert (1905–2001).

paleontologic methods and the validity of generalizations secured by paleontologists. A meeting of minds working along the boundary of these two fields, that of laboratory studies of the dynamics of short-range changes, and that of the accumulation and analysis of some of the results of long-range changes, was recognized as holding real promise.

It was agreed that interested workers in genetics and paleontology should be brought together in a committee, preferably of the National Research Council, for mutual enlightenment concerning the factual basis of theoretical concepts and interpretations. These workers seem to fall geographically into two groups: one with primarily zoological interests in the East, and the other, with primarily botanical interests, in the West. The following tentative list of potential participants suggested itself: [1|2] [The tentative list, placed here in the original, has been removed by Cain and placed in Table A1.1.]

Accordingly, upon the recommendations of Professor Bucher, the Administrative Committee of the Division of Geology and Geography of the National Research Council, on February 6, 1943, officially established a Committee on Common Problems of Genetics and Paleontology, with Dr. Simpson as chairman of the whole committee. Dr. Dobzhansky as chairman of the subcommittee on Genetics and Dr. Jepsen as chairman of the subcommittee on Paleontology.

After careful consideration, in conference with Dr. Ross G. Harrison, the chairman of the National Research Council, and Dr. Robert Griggs, chairman of the Division of Biology, it was decided to make this a *joint committee* of the Divisions of Geology and of Biology, placed, however, under the control of the Division of Geology and Geography. The committee was granted the sum of \$500 for the travel expenses necessary to bring about two group meetings, one in New York or Cold Spring Harbor, the other in San Francisco. This sum has been appropriated for the current fiscal year.

The undersigned, acting for Doctor Simpson, accordingly suggest that the participants plan to meet in June of the current year for two or more days, the Eastern group to assemble at Cold Spring Harbor, the Western group presumably in Berkeley or some other convenient place to be agreed upon. As possible topics, at least for the Eastern group, they suggest the following: [2|3] [The list of possible topics, placed here in the original, has been removed by Cain and placed in Table A1.2.]

We hope most sincerely that you will find it possible to accept membership in this committee and participate in the planned meetings. As the time is running short, we should appreciate an early reply. We are enclosing a stamped envelope for your comments and your answers (assuming you can accept the invitation) to the following questions:

1) What date or dates will be most suitable to you for a meeting in June?

2) How many days should the meeting occupy?

3) Will you please number in the order of their interest to you the topics in the list above.

4) Which of the topics listed would you be willing to discuss at the June meeting?

5) What additional topics should be discussed at the first or at subsequent meetings?

Very truly yours,

Th. Dobzhansky, Chairman /
Subcommittee on Genetics

Glenn Jepsen, Chairman /
Subcommittee on Paleontology

Walter H. Bucher, Chairman /
Division of Geology

WHB:C

[end of text]

TABLE A1.1

“Tentative List” of Committee Members, as it appeared in 26 February 1943 recruiting letter from Dobzhansky, Jepsen, and Bucher. This list can be compared with the membership of the Committee when constituted, as listed in Table 1.

Eastern Center—Zoological Outlook

Genetics

Demerec, M. (Cold Spring Harbor, N.Y.)
 Dobzhansky, Th. (Columbia Univ.)
 Dunn, L.C. (Columbia University)
 Mayr, Ernst (American Museum of Natural History, N.Y.)
 Muller, H.J. (Amherst)
 Wright, Sewall (Chicago)
 Cooper, Kenneth (Princeton)

Paleontology

- 1) Vertebrate:
 Colbert, E.H. (American Museum of Natural History, N.Y.)
 Romer, A.S. (Harvard Univ.)
 Jepsen, Glenn (Princeton)
 Simpson, G.G. (American Museum of Natural History, N.Y.)
 Wood, H.E. (Newark, N. J.)
- 2) Invertebrate:
 Caster, N.E. (Cincinnati)
 Patterson, Bryan (Chicago, Field Museum)
 Phleger, F.B. (Amherst)
 Cooper, G. Arthur (Smithsonian Institute [sic])

Western Center —Botanical Outlook¹³⁶

[*Genetics*]

Babcock, E.B. (Berkeley)
 Clausen, J. (Stanford)
 Epling, C. (Los Angeles)
 Stebbins, G.L., Jr. (Berkeley)

[*Paleontology*]

Axelrod, D.I. (Berkeley)
 Chaney, R.W. (Berkeley)
 Elias, M.K. (Lincoln, Nebr.)

136. The original letter transposed members of the sections within the Western Group: Axelrod, et al. were wrongly listed as geneticists; Babcock, et al. were wrongly listed as paleontologists. This is corrected here. Bold and italics added by Cain.

TABLE A1.2	
List of Possible Topics for Committee Attention, as it appeared in 26 February 1943 recruiting letter from Dobzhansky, Jepsen, and Bucher.	
<i>Genetics</i>	<i>Paleontology</i>
1. Geographic variation	
Gene gradients, gene flow	Faunal migrations, range changes, dispersal facilities
2. Discontinuity	
Genetic basis of race and species concepts, isolating mechanisms	Local populations, subspecies, "mutations," evolutionary steps
3. Evolutionary trends	
Possible genetic backgrounds and possible causation	Paleontological evidence for "orthogenesis" and related phenomena
4. Rate of evolution	
Variability of mutation rates in strains of a species and different species. Genetic control of mutation processes	Rapid evolution, "primitive relics," evolutionary stagnation

APPENDIX 2

Committee Mailing List

[This mailing list accompanied *Bulletin* 1, dated 15 May 1944, and bore the header, "National Research Council / Committee on Common Problems of Genetics, Paleontology and Systematics / *Mailing List*". Adjustments from the membership proposed in the 26 February 1943 recruiting letter are described in 1 June 1943 "Report of the Committee on Common Problems of Genetics and Paleontology," in Simpson Papers, folder: "National Research Council (Committee on Common Problems ...), #1".]

Prof. Edgar *Anderson*, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis, Mo.

Prof. Ernest B. *Babcock*, College of Agriculture, University of California, Berkeley 4, Calif.

Prof. Walter *Bucher*, Dept. of Geology, Columbia University, New York 27, N.Y.

Prof. Kenneth E. *Caster*, Dept. of Geology, University of Cincinnati, Cincinnati, Ohio

Prof. Ralph W. *Chaney*, Hearst Mining Bldg., University of California, Berkeley 4, Calif.

Prof. Bruce L. *Clark*, Hearst Mining Bldg., University of California, Berkeley 4, Calif.

Dr. Edwin H. *Colbert*, American Museum of Natural History, New York 24, N.Y.

Dr. G.A. *Cooper*, Division of Geology, U.S. National Museum, Washington, D.C.

Prof. Kenneth W. *Cooper*, Dept. of Biology, Princeton University, Princeton, N.J.

Dr. M. *Demerec*, Dept. of Genetics, Carnegie Institution, Cold Spring Harbor, Long Island, N.Y.

Prof. Th. *Dobzhansky*, Dept. of Zoology, Columbia University, New York 27, N.Y.

Prof. Carl O. *Dunbar*, Peabody Museum, Yale University, New Haven, Conn.

Dr. M. K. *Elias*, Nebraska Geological Survey, University of Nebraska, Lincoln, Neb.

Prof. Carl *Epling*, Dept. of Botany, University of California at Los Angeles, Los Angeles, Calif.

Dr. Myron *Gordon*, American Museum of Natural History, New York 24, N.Y.

Prof. Glenn *Jepsen*, Dept. of Geology, Princeton University, Princeton, N.J.

Prof. Herbert L. *Mason*, Dept. of Botany, University of California, Berkeley 4, Calif.

Dr. Ernst *Mayr*, American Museum of Natural History, New York 24, N.Y.

Prof. H. J. *Muller*, Dept. of Biology, Amherst College, Amherst, Mass.

Dr. Bryan *Patterson*, Curator of Paleontology, Chicago Museum of Natural History, Chicago, Ill. [1|2]

Prof. F. B. *Phleger*, Dept. of Geology, Amherst College, Amherst, Mass.

Dr. Alfred S. *Romer*, Dept. of Zoology, Harvard University, Cambridge, Mass.

Dr. George Gaylord *Simpson*, American Museum of Natural History, New York 24, N.Y.

DR.W. P. *Spencer*, College of Wooster, Wooster, Ohio

Dr. G. Ledyard *Stebbins*, Jr., College of Agriculture, University of California, Berkeley 4, Calif.

Prof. Curt *Stern*, Dept. of Biology, University of Rochester, Rochester, N.Y.

Prof. Chester *Stock*, Dept. of Geology, California Institute of Technology, Pasadena, Calif.

Dr. Horace E. *Wood*, Dept. of Biology, University of Newark, Newark, N.J.

Dr. Sewall *Wright*, Dept. of Zoology, University of Chicago, Chicago, Ill.

Please notify Dr. Mayr if you discover any errors or ommissions [*sic*] in this mailing list.

[end of text]

APPENDIX 3

“Reading List in Genetics”

[At their July 1943 meeting, the Eastern Section agreed to prepare several short bibliographies “as basic reading for the workers who wish to brush up on modern developments in the other field.” Curt Stern and Kenneth Cooper are listed to prepare bibliographies for genetics; Romer agreed for paleontology (see the *Report of Meetings*, p. 9). These failed to appear. Before February 1946, Dobzhansky, Simpson, and Mayr agreed to produce these reading lists. Their annotated bibliographies circulated to Committee members with *Bulletin 5*.]

[This source for this two-page mimeographed circular is located in NAS Archives, folder: “Geology and Geography 1946 / Committee on Common Problems of Genetics, Paleontology and Systematics / Jt. w/ Division of Biology and Agriculture.” A draft typescript, perhaps the original produced by Dobzhansky is located in Simpson Papers, folder: “National Research Council (Committee on Common Problems ...) #3”. Italics are added to titles by Cain.]

Reading List in Genetics

[by Theodosius Dobzhansky]

Genetics occupies a rather special place among the biological disciplines in that it contains relatively little descriptive matter. The core of genetics consists of a limited number of fundamental concepts or “laws”, which permit formulation of many deductive propositions which then serve as working hypotheses which can be tested by application to concrete situations encountered by observation or devised in experiments. It may even be possible, although it has not been tried, to write an outline of genetics in a way somewhat resembling geometry, building up on the basis of a few statements treated as “axioms”. In any case, learning genetics involves not only (or not so much) memorizing a body of facts but also acquisition of a habit of thinking in terms of certain genetic concepts. It is partly for this reason that most textbooks of genetics offer to the student “problems” for exercise.

Modern genetics has at least two intertwining branches: developmental genetics and population genetics. Although paleontologists and systematists will probably find both branches of interest in connection with their own work, it is the population genetics that concerns them more immediately. All the general textbooks of genetics cover both the developmental and the populational aspects, so that the readers whose interest is centered on one of them may find it expedient to concentrate on some chapters more than on others.

Colin, E. C. 1941. *Elements of Genetics* (Blakiston). This is probably the most suitable among the shorter textbooks. Presentation excel-

lent, very simple and at the same time adequate. Uses human illustrative material whenever possible, and is weak in parts dealing with exclusively botanical phenomena. Those particularly interested in population genetics will want to supplement this book by reading some chapters dealing with the problem of gene frequencies in some other book. [Colin 1941]

Dahlberg, G. 1942. *Race, Reason, and Rubbish* (Columbia University Press). This is not a textbook of genetics but a popular book aiming to combat race bias. It gives, however, a very concise outline of the fundamentals of genetics, especially of the populational aspects. [Dahlberg 1942]

Dobzhansky, Th. 1942 [*sic*: 1941]. *Genetics and the Origin of Species*. (2nd Edition Columbia University Press). An outline of population genetics which takes for granted a knowledge of the elementary facts. [Dobzhansky 1941]

Goldschmidt, R. 1940. *The material basis of evolution*. (Yale University Press). An examination of the evidence for evolution derived from many fields (genetics, systematics, comparative morphology, etc.) from the standpoint of one of the most eminent living geneticists. Propounds the view that there is a sharp distinction between “microevolution” and “macroevolution”, the latter being due to the so called “systemic mutations”. Although this view is shared by very few, if any, other geneticists or biologists, the book is most thought-provoking reading which a paleontologist will probably find interesting. [Goldschmidt 1940] [1][2]

Morgan, T. H., A. H. Sturtevant, H.J. Muller, and C. B. Bridges, 1915–1922.¹³⁷ (Henry Holt). Although, of course, very antiquated as an outline of genetics, this book remains a very good introduction to the basic facts and concepts. [Morgan, et al. 1915]

Sinnott, E. W., and L.C. Dunn, 1939. *Principles of Genetics* (3rd Edition, McGraw-Hill). This and the following book (Snyder) are the most widely used university textbooks of genetics. Sinnott and Dunn are particularly thorough in their treatment of the developmental aspects. Presentation finely balanced in giving equal prominence to zoological and botanical examples. [Sinnott and Dunn 1939]

Snyder, L. H. 1940. *The principles of heredity*. (2nd Edition, D. C. Heath). Emphasizes the zoological and particularly the human materials and aspects, and gives somewhat more attention to populational problems than other textbooks do. [Snyder 1940]

Th. D.
[end of text]

137. Dobzhansky omitted the title, *The Mechanism of Mendelian Heredity*. He makes reference to two editions.

APPENDIX 4

“Reading List in Paleontology”

[As with the “Reading List in Genetics,” this annotated bibliography was requested at the Committee’s July 1943 meeting of the Eastern Section. Romer agreed to produce this list (see the *Report of Meetings*, p. 9), but failed to deliver. Simpson produced the bibliography that circulated with *Bulletin 5*.]

[This source for this two-page mimeographed circular is located in NAS Archives, folder: “Geology and Geography 1946 / Committee on Common Problems of Genetics, Paleontology and Systematics / Jt. w/ Division of Biology and Agriculture.” A draft typescript, perhaps the original produced by Simpson is located in Simpson Papers, folder: “National Research Council (Committee on Common Problems ...) #3.” Italics are added to titles by Cain.]

Reading List in Paleontology
[by George Gaylord Simpson]

This brief list is compiled as an aid for geneticists and neontologists who wish to obtain an elementary but working knowledge of the data, methods, and theories of paleontology. These are all summary volumes, sufficiently technical for the mature biologist, but presupposing little or no¹³⁸ specialized knowledge of paleontology. It hardly needs to be said that there are many other books that could be consulted with profit, or that the important original contributions are scattered in thousands of technical books and papers. There are also some very valuable general works in French and German, not cited because the field is sufficiently represented for present purposes in these references written in English.

Darrah, W. C. 1939. *Textbook of paleobotany*. Appleton-Century. An adequate general introduction to the evolution of fossil plants. [Darrah 1939]

Lull, R. S. 1929. *Organic evolution*. Revised edition. Macmillan. Includes statements of the orthodox morphogenetic rules of paleontology, with examples. [Lull 1929]

Matthew, W. D. 1928. *Outline and general principles of the history of life*. Univ. of California. This course syllabus remains outstanding as a synthesis of many of the biological aspects of paleontology. [Matthew 1928]

Romer, A.S. 1945. *Vertebrate paleontology*. Revised edition [*sic*: “Second edition”]. Univ. of Chicago. Descriptive and phylogenetic, the

138. The word “no” is handwritten on the source.

- best available general taxonomic study of fossil vertebrates. [Romer 1945]
- Schuchert, C., and C. O. Dunbar, 1941. *A textbook of geology. Part II—Historical geology*. 4th edition. Wiley. Comprehension of paleontology also requires knowledge of the main elements of historical geology. This is an excellent text for this purpose, and includes summaries of the life of each geological period. [Schuchert and Dunbar 1941]
- Scott, W. B. 1937. *A history of land mammals in the Western Hemisphere*. Revised edition. Macmillan. An unusually full and readable study of faunal succession, intermigration, and phylogeny in the Americas. Brief discussion of some of the evolutionary principles involved. [Scott 1937]
- Shimer, H. W. 1933. *An introduction to the study of fossils*. Revised edition. Macmillan. Includes plants, invertebrates, and vertebrates. Mainly descriptive and necessarily rather superficial, but useful for broadest orientation. [Shimer 1933]
- Simpson, G. G. 1944. *Tempo and mode in evolution*. Columbia. An attempt to interpret, with the aid of genetical theory, phenomena of rate, inertia, momentum, adaptation, phyletic pattern, etc., as exemplified by paleontological sequences. [Simpson 1944] [1][2]
- Swannerton, H. H. 1930. *Outlines of paleontology*. 2nd edition. Arnold, London. Of value for its dynamic point of view, considering paleontology as the history of constantly evolving forms of life, with broad theoretical implications. [Swannerton 1930]
- Twenhofel, W.H., and R. R. Shrock. 1935. *Invertebrate paleontology*. McGraw-Hill. Somewhat unreliable in detail, but a useful and readily available summary of fossil invertebrates. [Twenhofel and Shrock 1935]
- Zittel, K. A. von. 1913–1932. *Textbook of paleontology*. Macmillan. Translated by C. R. Eastman and others, Vols. II and III revised by A. Smith Woodward. [von Zittel 1913–1932]
 Vol. I (Invertebrates), 2nd edition, 1913.
 Vol. II (Vertebrates except mammals), 2nd edition, 1932.
 Vol. III (Mammals), revised edition, 1925.

These unreadable and out-of-date volumes are nevertheless indispensable for reference as a sort of dictionary of the names and chief characters of most of the known fossil genera.

G. G. S.
 [end of text]

APPENDIX 5

“Reading List in Systematics”

[An annotated bibliography for systematics was not requested at the July 1943 meeting of the Committee’s eastern section, but Mayr produced one to accompany the bibliographies for genetics and paleontology when they were prepared for circulation with *Bulletin 5* for February 1946.]

[This source for this two-page mimeographed circular is located in NAS Archives, folder: “Geology and Geography 1946 / Committee on Common Problems of Genetics, Paleontology and Systematics / Jt. w/ Division of Biology and Agriculture.” Italics are added to titles by Cain.]

Reading List in Systematics

[by Ernst Mayr]

It is well known that during the first thirty years of this century most taxonomists were opposed to the tenets of the geneticists. This is not the place to analyze the reasons for this past conflict, the fact remains that much of the taxonomic work of that period had a strong Lamarckian flavor. This is true, for example, for Rensch’s pioneer study on geographical speciation (1929). The first edition (1937) of Dobzhansky’s *Genetics and the Origin of Species* showed conclusively that the findings of modern genetics were fully adequate to explain the observations of the taxonomist and has made the more recent summaries of various taxonomists possible.

General [readings]

- Bogert, C. M. et al. 1943. Criteria for vertebrate subspecies, species, and genera. *Annals. N.Y. Acad. Sci.*, vol. XLIV, pp. 105–188 [Bogert, et al. 1943]. A discussion by E. R. Dunn, C. L. Hubbs, E. Mayr, G. G. Simpson, and others on the significance of these categories.
- Camp, W. H., and C. L. Gilly, 1943. The structure and origin of species (in plants). *Brittonia*, 4, pp. 323–385 [Camp and Gilly 1943]. A single sample from the botanical literature showing the infinitely greater variety of species-like natural units among plants.
- Darwin, C. 1859. *On the origin of species* [Darwin 1859]. Darwin’s work was largely based on the studies of taxonomists. It is still eminently readable today, particularly in the chapters that deal with systematics.
- Huxley, J. (editor) 1940. *The new systematics*. Oxford, 583 pp. [Huxley 1940] The twenty-three contributors to this volume discuss various aspects of taxonomy and speciation in the plant and animal kingdom.
- Huxley, J. 1942. *Evolution: the modern synthesis* [Huxley 1942]. Contains a remarkable compilation of data derived from the work of taxonomists, but falls somewhat short of the goal of a “synthesis”.

- Mayr, E. 1942. *Systematics and the origin of species*. Columbia University Press [Mayr 1942]. A presentation of the methods of taxonomy and of the process of speciation as seen by the animal systematists, with a chapter on higher categories.
- Rensch, B. 1929. *Das Prinzip geographischer Rassen-Kreise und das Problem der Artbildung* [Rensch 1929]. The first comprehensive treatment of the principles of geographic speciation.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85, pp. 1–350 [Simpson 1945b]. A discussion of the relation between phylogeny and classification, of taxonomic categories and related subjects. [1|2]

Special [readings]

To gain a real insight into the working methods and principles of taxonomy nothing is more useful than a study of sound monographs and taxonomic revisions. See, for example, the papers by A. H. Miller (1941), Gloyd (1940), Hubbell (1936), and Welch (1938), listed in the bibliography of Mayr (1942).

The rapprochement between modern taxonomy and population genetics is so complete that there is very little difference of procedure between a good taxonomic analysis, such as that of Moore (1944) and a genetical-geographical analysis, as that of Dobzhansky (1944).

- Dobzhansky, Th. 1944. Chromosomal races in *D. pseudoobscura* and *D. persimilis*. Carnegie Inst. Pub. 554, pp. 47–144. [Dobzhansky 1944]
- Moore, J. A. 1944. Geographic variation in *Rana pipiens* Schreber of eastern North America. *Bull. Amer. Mus. Nat. Hist.*, 82, pp. 345–370. [Moore 1944]

E. M.
[end of text]

APPENDIX 6

Questionnaire

[This one-page mimeographed questionnaire was circulated as a blank and accompanied *Bulletin 5*. It bears no title other than the letterhead "National Research Council / Committee on Common Problems of Genetics, Paleontology and Systematics." An original questionnaire is preserved in Simpson Papers, folder: "National Research Council (Committee on Common Problems ...) #3."]

[Questionnaire]

(Please fill out this form, or discuss the same subjects more fully in a letter, and return as soon as possible to G. G. Simpson.)

I favor the following general topics for the proposed symposium to be arranged by the Committee (check those favored, or write remarks to right of each):

1. Rates of evolution.
2. Evolutionary trends.
3. Discontinuity.
4. Geographic variation.
5. Adaptation.
6. Other (specify).

Under those general topics favored for the symposium, I suggest the following specific subjects or titles. (If possible, give for each the name of a student who is competent and who might be willing to prepare a contribution on this subject.)

[space provided to enter information]

I would undertake (1) to prepare a paper or (2) to participate in discussion of a paper on these subjects for the symposium:

[space provided to enter information]

In addition to members of this Committee, I suggest that the following be invited to attend or participate in the proposed conference:

[space provided to enter information]

(Signed) _____

[for respondent]

[end of text]

APPENDIX 7

“Reading List on Paleobotany”

[This reading list was circulated with *Bulletin* 6, appended as pp. 6–7. The author was Maxim Konradovich Elias (1889–1982). The surviving correspondence for the Committee shows no request for this bibliography. It probably arrived unsolicited from Elias following *Bulletin* 5, with its reading lists for genetics, paleontology, and systematics. Elias likely believed paleobotany was underrepresented in the other reading lists and offered a remedy. Simpson probably wrote the introductory paragraph. Italics are added to titles and removed from author names by Cain.]

Reading List on Paleobotany [by Maxim Elias]

Supplementing the more general reading lists already distributed, the following list on paleobotany has been submitted by M. K. Elias, with his annotations. He has arranged the list in sequence from more popular to more technical, concluding with a few works on particular subdivisions of this large subject.

1. A. C. Noe. 1931. *Ferns, Fossils and Fuel*. Follett Publ. Co., Chicago.¹³⁹ Excellent brief (127 pp.) introduction to scientific and economic paleobotany. Includes review of origin of modern food plants.
2. John Walton. 1940. *An introduction to the study of fossil plants*. A. and Ch. Black, London. Somewhat more comprehensive (188 pp.) and up-to-date semi-popular account, excellently illustrated.
3. A. C. Seward. 1931. *Plant life through the ages*. Cambridge University Press. [Seward 1941 is a later edition.] Most comprehensive (601 pp.) and not too technically written summary on plant evolution and distribution through geologic time. Extensive bibliography and good index at the end of the book. However, Cenozoic vegetation is much less completely reviewed than Paleozoic and Mesozoic; the important Kuznetsk coal basin Carboniferous, Permian, Triassic and Jurassic floras of southwestern Asiatic Russia (p. 248) are erroneously referred to the Permian only; and no information is given on fossil grasses and other herbs.
4. E. W. Berry. 1923. *Tree ancestors*. Williams and Wilkins, Baltimore, (270 pp.) Interestingly written and fairly informative, but somewhat uncritical, and illustrated only by generalized sketches of angiospermic and gymnospermic remains, mostly leaves.

139. The draft version of this reading list names T. S. Rochweel Co., Chicago, as publisher.

Indispensable for a paleobotanist are:

5. F. O. Bower. 1935. *Primitive land plants*. MacMillan, London. (646 pp.) Comprehensive “essay on living plants as illuminated by fossils,” covering only vascular cryptogams. [6|7]
6. A. C. Seward. 1898–1919. *Fossil Plants*. Cambridge University Press, in 4 volumes, only fossil cryptogams and gymnosperms comprehensively treated.
7. Max Hirmer. 1927. *Handbuch der Palaobotänik*. R. Oldenburg, München und Berlin. (708 pp.) Excellent supplement to Seward’s “Fossil Plants,” profusely illustrated, mostly by original photographs and sketches. Particularly valuable because it includes:
8. Julius Pia (1927). Thallophyta; p. 31–136. Not very critical, but the only complete and well illustrated summary on fossil algae and fungi, and:
9. Wilhelm Troll (1927). Bryophyta, p. 137–146, well illustrated.
10. W. P. Shimper and A. Schenk. 1890. *Palaeophytologie*. Vol. 2 of Zittel’s *Handbuch der Palaeontologie*. Good summary on mostly European fossil floras, particularly gymnosperms and angiosperms, to which little attention is given in nearly all other text-books on paleobotany.
11. Agnes Arber. 1934. *Gramineae*. Cambridge University Press. Most complete and modern treatise on living grasses.
12. M.K. Elias. 1934. Tertiary prairie grasses and other herbs from the high plains. *Geol. Soc. Am. Spec. Pap.* 41. [Elias 1942] The only source on fossil prairie vegetation in the light of its living representatives, with bibliography and review on fossil herbaceous angiosperms.

[end of text]

APPENDIX 8

Abbreviations for Archive Materials

AMNH Archives: Department of Library Services, Special Collections, American Museum of Natural History, New York, NY.

Dunn Papers: Leslie Dunn Papers, APS Library, Philadelphia, PA.

Mayr Papers: Ernst Mayr Papers, Professional Correspondence, 1931–1952, Harvard University Archives, Cambridge, MA.

Mayr/Dobzhansky Papers: Correspondence between Ernst Mayr and Theodosius Dobzhansky, Series 2 of Theodosius Dobzhansky Papers, APS Library, Philadelphia, PA.

NAS Archives: National Academy of Sciences, collection for Division of Geology and Geography, Archives of the National Academy of Sciences, Washington, DC.

Simpson Papers: George Gaylord Simpson Papers, APS Library, Philadelphia, PA. All correspondence is located in series 1.

Sonneborn Papers: Tracey Sonneborn Papers, The Lilly Library, Indiana University, Bloomington, Indiana. Unless otherwise noted, the folder is series 5, box 8, “Princeton Bicentennial, Jan. 2–4, 1947.”

SSE Papers: Society for the Study of Evolution Papers, APS Library, Philadelphia, PA. These are the editor’s records for *Evolution*.

Stern Papers: Curt Stern Papers, APS Library, Philadelphia, PA.

Wright Papers: Sewall Wright Papers, APS Library, Philadelphia, PA.

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NAME INDEX

- Amadon, D., 11 (n. 87)
 Anderson, E., 1, 6, 26, 113, 125
 Arber, A., 106, 136
 Axelrod, D. I., 122
- Babcock, E. B., xx, 1, 6, 26, 30–31, 58,
 88, 104, 116, 117, 122, 125
 abstract, xxxv
 author, 27–29, 70–74, 107
- Balder, C. M., 119
 Baur, E., 43
 Beal, J. M., 113
 Berry, E. W., 90, 135
 Bogert, C. M., 131
 Bower, F. O., 136
 Bridges, C., 79, 128
 Bucher, W. H., xi, xv, xvii–xix, xxvii, 7,
 9, 11, 87, 119–121, 122, 125
 Burrows, W., 113
- Camp, W. H., 23, 131
 Caster, K. E., 7, 8, 122, 125
 addressee, 46
 author, 47–48
 Cattell, J., xxviii
 Chandler, E. J., 105
 Chaney, R. W., xxiii, xxx (n. 53), 1, 3, 6,
 27, 29–30, 53–55, 103–104, 118,
 122, 125
 abstract, 1–2
 addressee, 20–21, 24–26
 author, 21–24
 Clark, B. L., xxxvi (n. 76), 6, 125
 Clausen, J., xxxvi (n. 75), 31, 44, 122
 Colbert, E. H., 7, 8, 63, 66, 67 (n. 105),
 88, 96 (n. 118), 100 (n. 119), 102,
 116, 119, 122, 125
 abstract, 11, 14
 addressee, 34, 67–70
 author, 35–39, 95–96
 Cole, L. J., 113
 Colin, E. C., 127
 Cooper, G. A., 122, 125
 Cooper, K. W., xxix, xxx (n. 52), 7, 9, 10,
 114 (n. 129), 116, 122, 125
 Cuénot, L., 103
- Dahlberg, G., 128
 Darlington, C. D., 94
- Darwin, C., 131
 Davenport, C. D., 103
 De Vries, H., 42
 Demerec, M., 7–8, 79, 80, 82, 122, 125
 abstract, 14–15
 Dice, L. R., 113
 Dobzhansky, T., xii, xiii, xix–xx, xxii (n.
 20), xxiii, xxiv, xxvi, xxix, xxx,
 xxxv, 7 (n. 79), 10 (n. 85), 11, 43,
 65, 67, 74, 92–93, 99, 107, 113,
 115, 116, 118, 119–121, 122, 125,
 128, 132
 addressee, 21–24, 27–29, 29–34,
 53–58, 58, 63, 75–76, 103–107
 author, 20–21, 24–26, 76–78, 84–86
 concerns over organization of Prince-
 ton conference, xxx
 reading list, 10, 114, 127
 research in Brasil, xx (n. 17)
- Dodds, H., xxxi
 Dubinin, N. P., xxx, 43, 75, 76–77
 Dunbar, C. O., 7, 7 (n. 81), 9, 125, 130
 Dunn, E. R., 118, 131
 Dunn, L. C., xxxvi (n. 72), 119, 122, 128
 Durrah, W. C., 129
- Elias, M. K., 1, 10 (n. 85), 27, 31, 88,
 122, 125, 135–136
 abstract, 5–6
 addressee, 107
 author, 103–107
- Emerson, A. E., xi, xxiv, xxvi, xxxv, 113,
 117
- Epling, C., 1, 5, 20, 26, 27, 122, 125
 addressee, 91–95
 author, 53–58, 58–63
 conclusions on age of chromosome in-
 versions in *Drosophila* challenged
 by Mayr, 88, 88–91, 91–95, 96,
 97–100, 100–103
- Fisher, R. A., xi
 Florin, R., 71
- Gilly, C. L., 131
 Gloyd, H. K., 132
 Goldschmidt, R. B., xi, 63, 128
 Gordon, M., 7, 126
 Gregory, W. K., xvi

- Griggs, R., xviii (n. 11), 120
 Gulick, J. T., 94
- Haldane, J. B. S., xi, 104
 Harrison, R. G., 120
 Heer, O., 72
 Hiesey, W., 31
 Hirmer, M., 136
 Hopper, E. T., 88
 Hubbell, T. H., 132
 Hubbs, C., xxxv, 7 (n. 82), 131
 Hutchinson, G. E., xxxiii
 Huxley, J., xxvi, 8, 112–113, 131
- Ives, P. T., 77
 Jepsen, G. L., xiv, xvi, xvii–xix, xx, xxii, xxvii, xxvii (n. 36), xxix, xxx, xxxi (53), 7, 8, 11, 12–13, 115–116, 118, 119–121, 122, 126
 addressee, 47–48, 49–53
 author, 46, 48–49
 as proxy for Simpson, xxii, xix
- Johnson, M. L., 119
 Just, T., xxviii (n. 43)
- Keck, D., 31
 Kinsey, A. C., 113
 Knopf, A., xxx (n. 53)
 Krogman, W. M., 113
- Ladd, H. S., xvii (n. 12)
 Lewis, H., 60
 Linnaeus, C., 50
 Lull, R. S., 129
- MacGinitie, H. D., 27, 55
 Mampell, K., 79
 Mason, H. L., 1, 5, 22, 27, 126
 abstract, 4–5
 addressee, 70–74
 Matthew, W. D., xvi, 66, 129
 Mayr, E., xii, xiii, xvi, xx, xxii, xxiii–xxiv, xxvi, xxvii, xxix, xxx (n. 53), xxxiv, xxxv, xxxix–xl, 7, 8, 9 (n. 84), 10 (n. 85), 11, 13 (n. 88), 19–20, 41, 41 (n. 96), 67, 69, 84, 87–88, 89 (n. 116), 103 (n. 121), 113, 115, 116, 117, 118, 119, 122, 126, 131–132
 abstract, 12
 addressee, 35–39, 43–46, 48–49, 63–66, 88–91, 95–96, 97–100
 author, 34, 41–42, 49–53, 91–95, 100–103
 administrator of Genetics Section, xxii (n. 20)
 challenged by Stebbins, 89–91
 conclusions on age of chromosome inversions in *Drosophila* explained, 91–95
 creating *Bulletins*, xxiii, *Drosophila* research, 89 (n. 116)
 proxy for Dobzhansky, xx–xxii
 reading list, 10, 114, 131–132
 rise in community, xxxv
 role in Society for the Study of Evolution, 112–114, 118
 Mayr, Gretel (Margarete), xxxix
 McMinn, H. E., 31
 Metz, C. W., 84
 Miller, A. H., 27, 61, 132
 Moore, J. A., 132
 Morgan, T. H., xi, 42, 79, 128
 Muller, H. J., 7, 9, 9 (n. 83), 46, 79, 118, 119, 122, 126, 128
 Muntzing, A., 26
- Neel, J., 79
 Noe, A. C., 135
- Osborn, H. F., xvi
 Ownbey, M., 26
- Painter, T. S., 79
 Parr, A., 7
 Patterson, B., xix, 7, 8, 11 (n. 87), 122, 126
 abstract, 11–12, 15–16
 Patterson, J. T., xxx, xxx (n. 52), 83, 117
 Phleger, F. B., 7, 8, 122, 126
 abstract, 12, 13
 Pia, J., 136
 Pilger, R., 71, 74
- Rensch, B., 131, 132
 Richards, A. G., xxiv (n. 28)
 Roe, A., xxviii (n. 42)
 Romer, A. S., xxx (n. 53), 7, 8, 10, 114 (n. 129), 119, 122, 126, 129
 abstract, 16, 17
 Rubey, W. W., 116
- Sauer, [unknown], 27
 Schenk, A., 136
 Schmidt, K. P., 113, 118
 Schuchert, C., 130
 Scott, W. B., xvi, xxvii, 130
 Seward, A. C., 72, 135, 136

- Sharsmith, C. W., 27
 Shimer, H. W., 130
 Shimper, W. P., 136
 Simpson, G. G., xi, xiii, xvi-xx, xxiv-xxv, xxvi, xxvii, xxviii, xxix, xxx, xxx (n. 53), xxxi, xxxv, xxxix-xl, 9, 10 (n. 85), 11, 51, 87 (n. 115), 119, 120, 122, 126, 130, 131, 132, 133
 author of whole *Bulletin*, 109-114, 115-118
 author, 87-88
 departure for military service (1942) xix (n. 14)
 reading list, 10, 114, 129
 return from military service (1944) 87, 87 (n. 115)
 Sinclair, W. J., xxvii
 Sinnott, E. W., 106, 128
 Snyder, L. H., 128
 Spencer, W. P., 7, 8, 75, 77-78, 126
 abstract, 16-17
 paper, 78-84
 Stebbins, G. Ledyard, Jr., xx, xxx (n. 53), xxxi, 1, 1 (n. 78), 2, 6, 26, 27, 88, 100 (n. 119), 103 (n. 121), 104, 122, 126
 addressee, 76-78, 100-103
 author, 29-34, 67-70, 75-76, 88-91, 97-100
 challenging Mayr's conclusions on age of chromosome inversions in *Drosophila*, 89
 Stern, C., xxii, xxiii, xxx (n. 53), 7, 8, 9, 9 (n. 84), 10, 114 (n. 129), 126, abstract, 13-14
 addressee, 41-42, 84-86
 author, 43-46
 Stock, C., 126
 Stone, J. W., 79
 Sturtevant, A. H., xxx (n. 52, 53), 43, 79, 80, 82, 128
 Swinnerton, H. H., 130

 Timofeff-Ressovsky, H. A., 82-83
 Timofeff-Ressovsky, N. V., 78, 82
 Tiniakov, G. G., 79
 Tobgy, H., 28
 Troll, W., 136
 Turesson, G., 102
 Twenhofel, W. H., xviii (n. 12), 130

 Waagen, W. H., 47 (n. 99)
 Walters (Mrs.), 28
 Walton, J., 135
 Weidenreich, F., 51
 Welch, D'A. A., 132
 Wolf, C. B., 5
 Wood, H. E., 2nd, xvi, xix, xxiv, 119, 122, 126
 Wright, S., xi, xviii, xxx (n. 53), 1 (n. 77), 34, 37, 68-69, 93, 113, 118, 122, 126
 author, 63-66

 Zimmerman, E. C., 94
 Zittel, K. A., von, 130
 Zuitin, A. I., 78

SPECIES INDEX

- Acer*, 32, *negundo*, 32
Aegilops, 32
Agastache, 57
 rugosa, 57
 scrophulariaefolia, 57
 urticifolia, 57
Alismataceae, 55
Alnus, 32
 incana, 32
 viridis, 32
Anemone, 55
Anthirrhinum, 43
Audibertia, 59

Baccharis, 90
Baiera, 72
Bromus, 32

Calochortus, 26
Calosphace, 55
Caltha, 55
Carpinus, 23
 caroliniana, 23
 grandis, 23
Ceanothus, 5, 31, 90, see also *Cerastes*
Cedrus, 72–73
Celtis, 106
Cerastes (section of *Ceanothus*), 5, 32
 arboreus, 32
 coeruleus, 32
Chimaphila, 90
 umbellata, 94
Chlamydomonas, 45
Clematis, 55
Comarostaphylis, 90
Corylus rostrata, 32
Crepis, 3, 27–29, 30, 31, 74, 104, 107
 capillaris, 29
 cretica, 28–29
 foetida, 29
 fuliginosa, 28–29
 gaditana, 29
 nana, 3
 neglecta, 28–29
Cupressus, 90
Cypripedium arietinum, 90

Delphinium, 60
 Hanseni, 60
 hesperium, 60

Drosophila xx, xxx, 5, 8, 15, 16, 69,
 74–75, 76–78, 78–84, 89 (n. 116),
 90, 95–96
 affinis, 80
 americana, 44
 ananassae, 80
 cardini, 76
 distribution pattern of gene arrange-
 ments, 88–90, 91–95, 96, 97–100,
 101–103
 funebis, 16, 78, 79–80, 82–83
 hydei, 16, 79–82
 immigrans, 17, 79–80, 82
 melanogaster, 16, 43, 44, 75–76,
 76–78, 79–80, 82–83
 persimilis, 79, 89, 91, 95
 polymorpha, 76
 pseudoobscura, 5, 43, 75–76, 76–78,
 80, 88–90, 91, 93, 94–95, 97–100,
 100–103, 109, 132
 pseudoobscura-persimilis ancestor, 95
 repleta, 83
 robusta, 16, 79–80
 simulans, 44, 80
 transversa, 17, 82
 virilis, 44, 80, 82, 83
 willistoni, 80
Ectoconus, 36
Eriope, 57
Euphractus, 8, 15

Fagus, 20, 23
 grandifolia, 20, 23
 pacifica, 20, 23
 washoensis, 23
Festuca, 32

Galericularia, 57
Gaultheria, 90
Gigantopithecus blacki, 51–52

Hipparion, 8, 11
Homo, 51–53
 erectus erectus, 51–52
 erectus mongoloideus, 52
 erectus pekinensis, 52–53
 erectus post-soloensis, 52
 erectus robustus, 51
 erectus soloensis, 51–53
 erectus-soloensis, 52

- palaeojavanicus*, 51–52
sapiens australicus, 51–52
sapiens wadjakensis, 51
Homo (Javanthropus) soloensis, 51
Hordeum, 32
Hydractinia, 45–46, 86
Hyptis arborea, 55
Hyptis, 55
Hyracotherium, 8, 12

Junco, 61

Labiatae, 55–56, 58
Lactuca, 31
Lambertiana, 74
 ayacahuite, 74
 monticola, 74
Launaea, 31
Lepechinia, 55, 57
Libocedrus, 71

Mahonia, 90
 fascicularis, 94
Malacothrix, 31
Mallophaga, 86
Meganthropus palaeojavanicus, 51
Microseris, 31
Myosurus, 55

Opuntia, 55

Pachycereus, 55
Papaver alpinum, 44
Pecopteris vestita, 6
Phoenocopsis, 72
Pinus, 4, 5, 70–74
 albicaulis, 59
 albicaulis, 74
 attenuata, 4
 Ayacahuite, 59
 contorta, 32, 59, 62
 excelsa, 59
 flexilis, 59, 74
 Lambertiana, 59
 masoni, 22
 monticola, 59
 muricata, 4–5, 22
 nigra var. *mauretanica*, 73
 Nordenskiöldi, 72
 ponderosa, 32, 59, 62
 pyrenaica ssp. *mauretanica*, 73

 radiata, 4
 remorata, 4–5
 resinosa, 73
 silvestris, 73
 strobilus, 59, 74
Pithecanthropus, 51
 erectus, 51
 robustus, 51
Platypoecilus, 7
Polygonum, 90
 arifolium, 90
 virginianum, 90
Populus tremuloides, 32
Potentilla glandulosa, 44
Prenanthes, 90
Prepinus, 72, 74
Pyrus hoffmanni, 22

Quercus dumosa, 32

Rana pipiens, 132
Ranalisma, 55
Ranunculus, 55
Rhus, 90

Salvia, 26, 55, 59
 apiana, 61, 62–63
 carnosa, 59, 61
 mellifera, 61, 62–63
Scorzonera, 31
Scutellaria, 55
Sequoiadendron giganteum, 32, 69
Sequoia, 20, 23, 32
 langsdoerffii, 20, 23
 sempervirens, 20, 23, 32
Sinanthropus, 53
Sophophora, 80, 83
Sphenodon, 38
Sphenophyllum, 6
Stachys, 57
Stipa, 31, 105
Stipeae (tribe), 6, 105–106
Stratiotes, 6, 105
 aloides, 105
Symplocarpus foetidus, 90

Teucrium, 57
Tillandsia, 55

Xiphophorus, 7

SUBJECT INDEX

- aard-vark, 36
- accidents of sampling, as evolutionary factor, 63
- adaptation, 33, 54, 92, 97, 98, 111, 130, 133
- adaptive radiation, 36–37, see radiation
- adaptively useful mutation, 86
- algae, 136
- allopolyploidy, 25
- American Association for the Advancement of Science, meeting, St Louis (30 March 1946) 113, 117
- angiosperms, 104, 135, 136
- anti-evolutionists, 25, 53
- apogams, 26
- apomicts, 31
- artificial transmutation by X-rays, 75, 79, 82
- associations (plants) 25
 - evolution of grasslands, 25, 31
- autopolyploidy, 25

- balancing evolutionary factors, 63–66
- Betulaceae, 2
- Biological Symposia, xxviii
- biometry, 8
- biosystematics group in San Francisco, xiii (n. 1)
- bobcat, 68
- bobcats vs. mountain lion, environments compared, 68
- borages, 105
- Boraginaceae, 33
- brachiopods, 46, 48
- Brasil, Dobzhansky's visit, xx
- breeding potential (as a measure of species demarcation), 61
- bromeliads (Bromeliaceae), 54, 55 see orchids
- Brontornithidae, 15

- cacti (Cactaceae), 54–55
- camels, 66, (abundance), 37
- canids, evolution, 35, 36
 - variability, 70
- carnivores, 68
 - evolutionary rates, 34, 35–36
- causal relationships, environmental change and evolutionary rate, 34, 36–37

- Cedrus* vs. *Pinus*, comparison, 72–73
- cenospecies, 63
- Cerastes* (subgenus), 31
- ceratopsian dinosaurs, 14
- chance, role in evolution, 53
- chromosome patterns (*Drosophila*), 89–90, 91–95, 96, 97–100, 100–103
- chromosomes, transformation, 28–29
- Cichorieae, 31
- climate as a factor in evolution, 54
- cline, 93
- coelenterates, 46
- Cold Spring Harbor, xxiv
- Columbia Biological Series, xiv
- Columbia University, Department of Zoology, 50th Anniversary, meeting (17 October 1942), xix, 119
- Committee on Marine Ecology as Related to Paleontology (National Research Council), xviii
- Committee on Common Problems, addition of systematics, 1944, xvi
 - as joint committee, xviii, 120
 - creating the *Bulletins*, xxiii–xxiv
- Eastern Section (membership), xxxvi, 122
- Eastern Section, abstracts from meeting, 1943, 7–11
- Eastern Section, xv, xxi, xxxv, 120, 122, 127
- exchanging PhD students, 11
- expanding distribution of *Bulletins*, 67
- final activity, xxv, xxxi–xxxii, 111–113, 117
- Genetics Section, xv, 121
- letter exchanges planned and instructions, xxii–xxiv, 19
- Mayr's role, 87
- meetings, 1943
- planning, xx, membership, xxxvi, 122, 125–126
- name change to include 'systematics', xvi, 19
- Paleontology Section, xv, 121
- progress and plans (November 1944), 87
- progress and plans (February 1946), 109
- publications, xxxvii

- purpose, 19–20, 24, 87, 109, 119–121
 reading lists, 10, 10 (n. 85), 127–128,
 129–130, 131–132, 135–136
 recruiting, 119
 regional meetings, 1943
Report of Meetings, 1943, xx–xxi
 Simpson's initial plan (abandoned)
 xviii–xix
 steering committee, 19–20, 41, 67–88
 temporary nature, terms for disband-
 ing, 111
 topics for attention, 123
 trio of paleontologists as original or-
 ganizers, xvi–xix
 use of Columbia University 50th An-
 niversary to plan activity, xix
 Western Section (membership) xxxvi,
 122
 Western Section, abstracts from meet-
 ing, 1943, 1–6
 Western Section, xv, xxi, 120, 122
 Committee on Common Problems of Ge-
 netics, Paleontology and Systemat-
 ics (name change, 1944) xvi, 19
 Committee on Paleoeecology (National
 Research Council) xviii (n. 112)
 Committee on the Application of Biologi-
 cal Data and Methods to Geological
 Problems, xxxii–xxxiii, 115 (n. 131)
 Committee on the Application of Physics
 and Chemistry to Geological Prob-
 lems, xxxiii
 comparing fossil and living species
 (botanical) 20–21
 competition (relative importance in plant
 vs. animal evolution) 33
 Compositae, 31, 33
 conference, planning, 110–111, 115–117,
 133
 conifers, historical and geographical dis-
 tribution, 70–74
 conservatism, evolutionary, 26, 38, 61, 106
 continental floras vs. insular faunas, 91
 continuity, genetic, 53
 correspondence as exploratory mecha-
 nism, 87, 109
 counter selection, 93
 cryptogams, 136
 Cyperaceae, 33

 danse macabre, 26
 Department of Zoology, Columbia Uni-
 versity, 50th Anniversary, meeting
 (17 October 1942) xix, 119

 dichobunids (related to leptchoerids) 38
 dicynodonts, 8, 16
 Dipsacaceae, 30
 discontinuity, 8, 12–14, 49, 93–94, 111,
 123, 133
 paleontological, 47, 49
 dispersal, 93–94, 98–100, 102–103, 123
 distribution, animals, 89, 95
 plants, 54–58, 88, 88–91, 91–95, 98
 divergence, 89–90
 drift genetic, 44, 86

 echinoderms, 46
 ecological balance (in fossil faunas), 37
 ecological niche, 85–86, 103, 105
 ecotype (in *Drosophila*), 102, ecotype (in
Potentilla), 44
 editorial notes
 effective breeding population as evolu-
 tionary factor, 34, 63, 69
 elephants (abundance), 37, 66
 environment as an evolutionary factor, 68
 epiphytes, see orchids and bromelids
 epiphytic flora, distribution and origin,
 30–31
 Equidae, 70
 Euphorbiaceae, 2
Evolution (journal), launch, xxvi
 potential sponsors, 112
 proposal and plans, 111–113, 118
 publish in Britain, 112
 evolutionary conservatism, 26, 38, 61, 106
 evolutionary opportunism, 75
 evolutionary stagnation, 68
 explosive evolutionary rates, 67
 extinction since other epochs in Tertiary
 (botanical), 21, 23
 since Pleistocene (botanical) 21, 22–23

 Fagaceae, 2
 faunal migration, 123
 faunal succession, 130
 felid evolution, 35, 36, 68, 70
 ferns, 135
 fissipede evolution, 35
 Flacourtiaceae, 30
 floras of North America, Pleistocene,
 20–21, 22, 88, 88–91, 91–95
 Tertiary, 20–21, 24, 25, 27–29, 29–34,
 53–58
 Florissant, 54
 foraminifera, 9
 fungi, 136
 Fusulinids, 9

- gaps in fossil record, 49
 gene arrangements (*Drosophila*) 89–90, 91–95, 96, 97–100, 100–103
 gene differences between individuals of same species, populations and species, 41–42, 43–46
 gene flow, 42, 45, 123
 gene gradients, 123
 gene mutations as evolutionary factor, 29
 genetic drift, 44, 86
 genetic isolation, 44–46
 genetic submergence in *Pinus remorata*, 5
 genetics, developmental, 127, 128
 laws of, 127
 population, 127, 128
 reading list, 10, 127–128
 textbooks, 127–128
 genic elimination by natural selection, 70
 geographic isolation, 84–86
 geographic race formation, 26, 84
 geographic range, 123
 geographic variation, 11–12, 111, 123, 133
 in *Pinus*, 70–74
 Geological Society of America, meeting (December 1941), xv
 meeting (December 1944), 119
 good neighbors program, US government, xx (n. 17)
 gradients, morphological or physiological, 29
 Gramineae, 33
 grasses, 136
 evolution of prairie, 105–107, 136
 Guttiferae, 30
 gymnosperms, 135, 136

 hackberry, 106
 herbs, Tertiary, 105
 heterozygosity, 42, 68, 69–70, 75
 hiatus in animal phylogenies, 47
 historical geology, 130
 horizontal vs. vertical species, 50
 horses, 8, 66, 96
 abundance, 37
 humans, early (Ventana Cave, Arizona), 96
 genes differences, 43
 human fossils (reclassified), 50–53
 human subspecies, 51–52
 hybrid swarm, 61
 hybridization, 79
 hybrids (intergeneric) in tropical orchids, 31

 ichthyosaurs, 66, 69
 abundance, 37
 immigration pressure, as evolutionary factor, 63
 inertia, 130
 insectivores (abundance), 37
 instantaneous evolution (almost) in felids, 35
 insular faunas vs. continental floras, 91
 interaction of evolutionary forces, 83
 intergeneric hybrids in tropical floras, 31
 intergradation, 29, 46, 59–60
 across major taxa, 46
 International Congress of Genetics, Sixth, 1932, 65
 introgression, 26, 62
 inversions, 81
 isolating mechanisms, 42, 84–86, 89 (n. 116), 90, 94, 123
 isolation as evolutionary factor, 29, 83, 86
 isolation, geographic vs. secular, 86
 origin of genetic, 44–46
 secular, 86
 spatial (as an evolutionary factor), 29

 Java human fossils, 52
 Jesup lectures (Stebbins), xxxi
 joint field common to genetics, paleontology, and systematics, 87
 Journal of Animal Taxonomy (proposed), xxiv
 journal, for continuing Committee activity, see *Evolution*

 karyotype evolution (in *Crepis*), 28–29

 Lamarckian evolution, 131
 lapsus calami, 104
 Lauraceae, 2
 Leguminosae, 2
 leptochorids (related to dichobunids), 38
 lethal vs. visible mutations, frequency in *Drosophila*, 75
 Linnaean taxonomy, 49
Lloydia for Princeton conference, xxviii
Lloydia symposium, 89 (n. 116), 109

 macroevolution, 47, 48, 50, 128
 macrogenesis, 46, 50
 as a hypothesis of despair, 47
 Madinae (tribe), 31
 maize, 15
 mammal-like reptiles, 36

- mathematical theory, 64–65
 Melastomaceae, 30
 Mendelian populations, evolution in (Wright), 64
 microevolution, 48, 128
 microgenesis, 46, 50
 migration in *Crepis*, 3, 27
 versus extinction or transformation, 21
 as an evolutionary factor, 29
 modernizer in paleontology, xvi
 mollusca, 46
 Moraceae, 2
 Morgan school of genetics, 42
 morphogenetic rules, 129
 morphologic gaps or breaks in evolutionary series, 46, 48
 mountain lion vs. bobcats, environments compared, 68
 multiple perspectives, xiii
 musk ox, 93, 96
 mutability, total in species, 34, 76
 mutation, adaptively useful, 86
 comparable rates in *Drosophila* species, 8, 76–78, 78–84
 discrepancies over meaning of term in genetics versus paleontology, 47
 inconspicuous, 42
 micro- vs. macro-, 42, 47–48, 48–49
 neutral, 86
 relative frequency of visible vs. lethal, 75, 79
 role in evolution of *Crepis*, 29
 systematic, 46, 128
 mutation finder, 77
 mutation rate as evolutionary factor, 16–17, 34, 63–66, 68, 69, 75, 76–78, 78–84, 86
 mutation theory (De Vries), 42
 mutator genes, 79
- National Research Council, Committee on marine ecology as related to paleontology, xviii
 Committee on Paleoecology, xviii (n. 112)
 Division of Biology and Agriculture, Division of Geology and Geography, Subcommittee on ecology of marine organisms, xviii (n. 12)
 willingness to sponsor journal, 112
 natural selection, 29, 33, 34, 44, 63, 68, 70, 74, 85, 86, 92, 97, 101–102
 direction, 64
 Neanderthals, 52–53
- neontology, neontologist (compared with paleontologists), 8, 49, 52
 neutral mutations, 86
 New York Academy of Sciences, xxviii
 New York circle, xiv, xxxv
 niche, ecological, 85–86, 103, 105
- opportunism, evolutionary, 75
 orchids (Orchidaceae), 30–31, 54, 55
 orthogenesis, 5, 123
 orthoselection, 9
 oyster, 45
- paleobotany, reading list, 10, 118, 135–136
 paleoecology, xviii
 paleontological discontinuity, 47
 paleontology, laws of, 129
 modernization, xvi
 reading list, 10, 129–130
 textbooks, 129
 parallel evolution, 8, 17, 53
 pelecypods, 48
 perspective analysis, xiii
 Phanerogams, 104
 Phororhacidae, 15
 Phororhacoid birds, 8
 phyletic patterns, 130
 phylogenetic patterns in *Crepis*, 28
Pinus, historical and geographical distribution, 70–74
Pinus vs. *Cedrus*, comparison, 72–73
 placental carnivores, 14
 Pleistocene climate, 102
 Pleistocene floras of North America, 20–21, 22, 88
 ploidy, cause of new species, 26, 29, 31, 42, 58
 frequency in animal groups, 42
 frequency in plant groups, 32
 polyploidy, 42, 59
 allo-, 25
 auto-, 25
 polytypic species, different causes in animals and plants, 61–63
 in *Agastache*, 57
 in *Crepis*, 27–29
 in modern tropical floras, 31
 in *Pinus*, 59
 in plant groups, 32
 in recent woody genera, 31
 polytypic species concept, 26, 50–53, 58–63
 polytypic species or polytypic complexes, 58, 59, 60–63, see Rassenkreis

- polyvalence, xiii, xxx (n. 49), xxxv
population size as an evolutionary factor, 68–69
porpoises (abundance), 37
prairie grasses, evolution of, 105–107, 136
preadaptation, 25, 32, 33, 70, 75
Princeton University bicentennial conference, xxvi–xxxii
 as climatic moment, xxxiv
 planning and program, 10, 115–117
 program committee (listed), 116
 questionnaire for conference planning, 133
Princeton University symposium volume, xxxii, 117
Psilopteridae, 15

questionnaire for Princeton bicentennial conference planning, 133
questionnaire, 116, 133

race, biological concepts, 123, geographic, 59, human, 128
race formation, geographic, 26, 84
radiation, of archosaurian reptiles, 36, of placental mammals, 37
random fixation, 68
Ranunculaceae, 55
rapid evolution, 32–33, 63, 66, 67–70, 76, 86, 106, 107
 in ceratopsians, 35, in felids, 35
Rassenkreis, 44, 132
rates, mutation, 68, 123, rapid, 123
rates of evolution, 1 (n. 77), 8, 14–17, 20–21, 32, 34, 35–39, 46, 47–48, 63–66, 67–70, 75, 88–91, 91–95, 106, 107, 110–11, 123, 130, 133
 caused by internal factors, 38, 68
 changes in the body of any one species, 36
 changes within one phyletic group, 35
 compared across groups, 32–33
 compared using ‘Sewall Wright formulae’, 34, 35–39
 inherent in phylogenetic lines, 38
reading list, 10, 10 (n. 85)
 genetics, 127
 paleobotany, 118, 135–136
 paleontology, 129–130
 plan, 114 (n. 129), 127
 systematics, 131
recombination as an evolutionary force, 68, 69–70

relic species, 32, 73
relics, 123
reproductive isolation, 61, 84–85
Rhynchocephalia, 38, 66
rodents, 88, abundance, 37
Rubiaceae, 30

Salicaceae, 2
saltation, 42, 86
sampling (effects of) as an evolutionary force, 68
Sandia Cave, 96
Sapotaceae, 30
Say’s ground squirrel, 96
selection pressure, 34, 63, see natural selection
selection, counter, 93
selective value of gene arrangements (in *Drosophila*), 92–93, 97, 101–102
sloths, 8, 16
slow evolution, 68
Society for the Study of Evolution, Boston meeting (December 1946) xxxi
 call for charter members, 118
 merger with Society for the Study of Speciation, 117–118
 officer list for 1946–1947, xxx (n. 52), 117–118
 organized, xxvi, 117–118
 proposal, xxiv, 111–113
Society for the Study of Speciation, xiii (n. 2), xxii (n. 20), xxiv
 bulletins, 113
 merger and disbanding, 113, 118
 organization, 113
Society of Vertebrate Paleontology, xvi (n. 7)
speciation, 81, 84–85
 examples, 88
 allopatric, 26, 45, 59
 sympatric, 45–46, 58–59, 84–86
species, interconnecting, 74
species as ‘good’ species, 25, 26
species concepts, genetic basis, 123
species formation by mutation, 42
species in the making, 32
species processes, comparing normal modes in zoology and botany, 26, 28, 31, 32
species processes, zoological, 26
species recognition (paleontological conventions for), 21–22, 24, 24–25
squirrel, 96

- stagnation, 26, 32, 33, 35, 69, 123
 Stipeae
 Subcommittee on Ecology of Marine Organisms (National Research Council), xviii (n. 12)
 subspecies, 123, 131
 sympatric speciation, 8, 9, 45–46, 59, 84–86
 sympatric species, 49–53, 59
 symposium (*Lloydia*), 109
 symposium volume (from Princeton bi-centennial conference), xxvii, 117
 synchronic species, 49–53
 synthesis, 131
 systematics, reading list, 10, 131
 systematics as “vital link”, xvi

 Taeniodonta, 8, 15
 tapir, 93, 96, 98
 taxonomic nomenclature, 49–50
 Tertiary floras of North America, 1–2, 3–6, 20–21, 24, 25, 27–29, 29–34, 53–58
 Thallophyta, 136
 thecodonts, 36
 total mutability, 34
 trading zone, xxxv
 transformation of chromosomes, 28–29
 transitional community or group, xvii, xxxiv
 trees, 135

 trends (evolutionary), 111, 123, 133
 Trinil Man, 52
 tropical floras in Cenozoic, changes to, 23–24, 29–30, 53–58

 uniformitarianism, 47

 Valerianaceae, 30
 Ventana Cave, 96
 vertical species, 49–53
 vertical vs. horizontal species, 50
 visible vs. lethal mutations, frequency in *Drosophila*, 75
 viverrid evolution, 35, 36
 viverrids (variability), 70

 Waagens or waagenation (unit of morphological change), 47, 48
 war conditions (effects on activity), 109–110
 Water-soldier, see *Stratiotes*
 weed species, 75, 77, also see pest species
 Williams Cave, 96
 Wright’s formulae, 34, 37–39, 63, 68–69
 also Sewall Wright formulae

 xerophytic flora and fauna (McKirkrick, California), 98

 zoogeography, 103

The Committee on Common Problems provided a crucial foothold for those seeking a synthetic view of evolution in 1940s America. These forgotten documents show the Committee at work: building coalitions, defining priorities, and negotiating a common vision. They also show factions within the Committee competing for the leadership of this emerging community.

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